Decomposition Dynamics, Carbon Sequestration, and Management, of Coarse Woody Debris in Eastern Australian Forest Ecosystems

Edward James Webber

Fenner School of Environment and Society

January 2008

A thesis submitted for the degree of

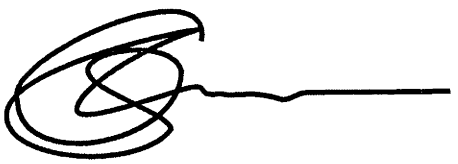
Doctor of Philosophy of The Australian National University

STATEMENT OF ORIGINALITY

I declare that this thesis represents an original piece of work, and does not contain, in part or in full, the published work of any other individual, except where acknowledged.

Some of the statistical analyses of Chapter 4 Section 2 (*Decay Rates*) were done by Dr. Ann Cowling and Emma Knight (Statistical Consulting Unit, The Australian National University).

Contributions from other individuals or organisations, including help with data collection or sample processing, professional advice, and access to sampling-sites, is detailed in the acknowledgements.



Edward Webber

The Australian National University

30th January 2008

ACKNOWLEDGEMENTS

I would like to thank my supervisors Assoc. Prof. Cris Brack, Mr. Ken Johnson, and my advisor Dr. Dave Hilbert.

I would also like to thank Dr. Ann Cowling, Dr. Jeff Wood, Dr. John Maindonald, and Emma Knight (Statistical Consulting Unit, The Australian National University) for assistance with the design and analyses of this project. I would also like thank the Statistical Consulting Unit (The Australian National University) for providing the many courses involving the design and analyses of experiments.

Assistance in the form of access to sampling sites was provided by many institutions. Forestry Tasmania (Dr. Simon Grove) provided access to southern Tasmanian eucalypt-forest sites, field equipment and field assistants, and staff to assist in laboratory processing of samples. Forests NSW (Ian Barnes) and NSW National Parks and Wildlife Service provided access to eucalypt forest sites in southern New South Wales, Department of Primary Industries and Fisheries (Dr. Steven Bray) provided access to eucalypt woodland sites in central Queensland. CSIRO Tropical Forest Research Centre (Dr. Dave Hilbert) and Queensland Parks and Wildlife Service provided access to tropical rainforest sites in Queensland. Forestry Tasmania, CSIRO Tropical Forest Research Centre, and Department of Primary Industries and Fisheries, through collaboration, also provided field assistance and transport. Forestry Tasmania also provided a grant toward my fieldwork costs whilst sampling in southern Tasmania.

I also would like to thank my collaborators Dr. Simon Grove (Forestry Tasmania; Tasmania), Dr. Steven Bray (Department of Primary Industries and Fisheries; Queensland), and Dr. Dave Hilbert (CSIRO Tropical Forest Research Centre; Queensland). A debt of gratitude is also owed to Mauro Davanzo (NSW), Lyle Reynolds, Gabriel Warren, Darren McNeill, Jacinta Lesek, and Alison Phillips (Tasmania), John Compton (central Queensland), and Matt Bradford (far north Queensland), whom all assisted me with either fieldwork or laboratory work. I would also like to thank Mike McLarin (Forestry Tasmania) for providing growth data for *Eucalyptus obliqua*, which was used in the modelling of carbon dynamics shown in the Discussion Chapter. I would also like to thank the many friendly and helpful staff of the Geeveston office of Forestry Tasmania for providing authorisation, and keys, to restricted areas allowing access to sampling-sites.

During this project, I became a student-member of the Cooperative Research Centre for Greenhouse Accounting, and I would like to thank the CRCGA for providing a top-up scholarship (without which I would not have been able to sample interstate), and access to information and resources that come with the privilege of being associated with the CRCGA.

Most of all, I would like to acknowledge the immense understanding and patience of my wife, Beryl, whom provided unending support and tolerance during this work.

Lastly, I would like to dedicate this work to my wife Beryl, and to two family members whom passed-away during this project, Noel Beilby and Bill Rigbye.

ABSTRACT

The contribution of coarse woody debris (CWD; logs lying on the ground) to ecosystem functioning and carbon sequestration has generally been ignored by ecologists. Most studies of CWD have involved the measuring of amount (volume or mass) in the ecosystem studied, with only a minority of studies assessing the decomposition dynamics of the CWD. Due to the low level of interest in Australian CWD, the decay dynamics of the eucalypts have been ignored in the past, and information requiring knowledge of eucalypt decomposition has been unavailable to ecosystem managers in Australia. This project targets this knowledge-gap, providing decay dynamics for four different ecosystem types incorporating a latitudinal-gradient along eastern Australia. The latitudinal-gradient incorporated four regions, which, from south to north were: (i) southern Tasmanian wet eucalypt forest, (ii) south coastal New South Wales wet eucalypt forest, (iii) central Queensland dry eucalypt woodland, and (iv) far north Queensland tropical rainforest. A chronosequence approach was used to provide samples of differing ages.

Decrease in sample wood-density (specific gravity) over time (sample age) was used to determine the rate of decay at the regional and sub-regional level. It was found that the eucalypts studied in the wet eucalypt forests were the slowest decaying angiosperm species known. The single-exponential model (SEM) decay-constant *k*-value for the *Eucalyptus obliqua* L'Hér. of southern Tasmania was 0.00723 yr^{-1}, and the *k*-value for the mixed *Eucalyptus* L'Hér. spp. of the south coastal region of New South Wales was calculated as 0.00554 yr^{-1}. The difference in the curves represented by these *k*-values, which represents a regional difference as well as species-difference, was non-significant ($p = 0.1585$). These *k*-values represent a $t_{0.95}$ (time to 95% loss of mass) of 414 yr and 541 yr respectively. Since the fitted SEM-curves for southern Tasmania and NSW were not significantly different, the data were combined, and produced a composite SEM *k*-value of 0.00662 yr^{-1}, which produces a $t_{0.95}$ of 453 yr. The SEM *k*-value for the studied mixed-species tropical rainforest of far north Queensland was 0.1121 yr^{-1}, which gives a $t_{0.95}$ of 26.7 yr. (It must be noted that the *k*-statistics were largely based on logs <45 cm diameter and larger material was too rare and too variable to produce reliable values. Also not that the tropical rainforest sites contained 81 species, in 30 families, with a wide variability in rates-of-decay, and the calculated *k*-value may be dominated by the long residence time of a few decay-resistant species, resulting in an

underestimation of the actual decay-rates of most species. Additionally, not all species were collected, so, due to the fast decay-rates of these rainforest species, a bias may be inherent in the increased probability of collection of longer-lasting species that are more decay-resistant.) The central Queensland woodland decay-rate analyses proved inconclusive, as a trend in decreasing wood-density could not be determined, despite samples of up to 41 yr age (since being felled) being collected. (This is undoubtedly an artefact of the harsh environment experienced in central Queensland; cool winters to extremely hot summers, and a generally very dry climate.)

The volume of CWD in the environment (loading) was measured using the line-intersect method (LIS). Corrections for slope were made to calculate loadings to equivalent values per horizontal area. Mean CWD volume-loadings were 7.7 m^3 ha^{-1} (central Queensland eucalypt woodland), 46.2 m^3 ha^{-1} (far north Queensland tropical rainforest), 51.5 m^3 ha^{-1} (southern coastal New South Wales wet eucalypt forest), and 731.7 m^3 ha^{-1} (southern Tasmanian wet eucalypt forest). Fifty-three 300 m triangular line-transects were run in southern Tasmania, with the 11 highest volume-loadings all exceeding 1000 m^3 ha^{-1}, with nine transects occurring in mature eucalypt forests (out of 45 transects) and the other two occurring in regrowth eucalypt forests with some mature trees (out of 8 transects); the highest loading for any transect was 2199.4 m^3 ha^{-1}. (These 'mature eucalypt forests' may be classified as 'old-growth' by some people, but are called 'mature' here, as old wet-forests have the eucalypt component replaced by rainforest; which existed as subordinate-vegetation in the earlier eucalypt-dominated forest ecosystem.)

CWD mass-loadings were 13.2 Mg ha^{-1} for the tropical rainforest of far north Queensland, 5.8 Mg ha^{-1} for the dry eucalypt woodland of central Queensland, and 26.7 and 342.8 Mg ha^{-1} for the wet eucalypt forests of NSW and southern Tasmania respectively. Assuming C content of CWD wood to be stable at 50% by mass, C-loadings of CWD were 6.6 Mg C ha^{-1} for the tropical rainforest of far north Queensland, 2.9 Mg C ha^{-1} for the eucalypt woodland of central Queensland, and 13.3 and 171.4 Mg C ha^{-1} for the wet eucalypt forests of NSW and southern Tasmania respectively.

Due to an inability to determine a SEM decay-model constant for the central Queensland CWD, this region did not have CWD carbon-release and carbon-retention calculated. Carbon release to the surrounding environment was calculated to be 738.4

kg C ha^{-1} yr^{-1} (0.738 4 Mg C ha^{-1} yr^{-1}), 73.80 kg C ha^{-1} yr^{-1} (0.073 80 Mg C ha^{-1} yr^{-1}), and 1.239 Mg C ha^{-1} yr^{-1} for the tropical rainforest of far north Queensland and the eucalypt forests of NSW and southern Tasmania respectively. Although the C emissions from the Tasmanian CWD are high by world standards, at 1.239 Mg C ha^{-1} yr^{-1}, the high mass loading coupled with the slow decay rate result in 170.2 Mg C ha^{-1} being retained within the CWD. (This is assuming a steady-state input into the CWD pool, over the long-term, at a regional level.) The wet coastal eucalypt forest of southern NSW, although subjected to CWD removal for fuel wood, retains 13.25 Mg C ha^{-1}; also assuming steady-state CWD input. The tropical rainforest retains 5.849 Mg C ha^{-1} of its C stored in CWD. This shows CWD to be an important component of forest C sequestration, especially in the wet eucalypt forests. If the burning of wood is counted as a source of C emission, then the retention of unburnt-CWD in forest ecosystems should be included as a form of C storage.

Modelling of southern Tasmanian *E. obliqua* showed that long-term accumulation of CWD could account for as much as 42% of the wood that is stored in the living trees. If a forest had been cleared of CWD (such as happens after post-logging site preparation), then allowing CWD to accumulate can be a considerable source of stored-carbon. In this scenario, if CWD is included as tradable-carbon, then it has the potential to provide substantial increases in income for forest managers/owners.

This study has shown that coarse woody debris is an important component of forest ecosystems that has been severely depleted below natural levels in the wet eucalypt forests of southern Australia, and it needs to be included in forest management policy. The potential for large increases in carbon-credits for a forest ecosystem if CWD is to be included in carbon-trading also gives this important ecosystem component a very high monetary-value as well as its high ecological-value in ecosystem functioning.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

INTRODUCTION

The contribution of coarse woody debris (CWD; logs lying on the ground) to ecosystem functioning and carbon sequestration has generally been ignored by ecologists. Most studies of CWD have involved the measuring of amount (volume or mass) in the ecosystem studied, with only a minority of studies assessing the decomposition dynamics of the CWD. Due to the low level of interest in Australian CWD, the decay dynamics of the eucalypts have been ignored in the past, and information requiring knowledge of eucalypt decomposition has been unavailable to ecosystem managers in Australia. This project targets this knowledge-gap, providing decay dynamics for four different ecosystem types incorporating a latitudinal-gradient along eastern Australia. The latitudinal-gradient incorporated four regions, which, from south to north were: (i) southern Tasmanian wet eucalypt forest, (ii) south coastal New South Wales wet eucalypt forest, (iii) central Queensland dry eucalypt woodland, and (iv) far north Queensland tropical rainforest.

1.1 WHY IS CWD IMPORTANT?

Coarse woody debris is an important, but generally ignored functional component of ecosystems, despite their conspicuous nature (Silvester *et al.* 1982; Harmon *et al.* 1986; Franklin *et al.* 1987; Schowalter 1992; Brown *et al.* 1998; Delaney *et al.* 1998; Schowalter *et al.* 1998; Chee 1999; Grove and Meggs 2003; Debeljak 2006). CWD contributes to forest structural complexity (Tinker and Knight 2001; Woldendorp *et al.* 2002a), and contributes to the health of the ecosystems through its role in ecosystem functioning (Larsen *et al.* 1978; Triska and Cromack 1980; Foster and Lang 1982; Franklin *et al.* 1987; Hodge and Peterken 1998; Tainter and McMinn 1999; Lindenmayer *et al.* 2000; Woldendorp *et al.* 2002a; Brown *et al.* 2003; Grove and Meggs 2003; Debeljak 2006). (In this thesis I use the term "ecosystem health" as a means of referring to ecosystem functionality – that is, it is referring to whether the ecosystem is functioning effectively in a natural manner, or if it is compromised in functioning in a natural manner.) However, in recent years there has been an increase in the awareness of the functional-importance of CWD (Chambers *et al.* 2000). There is generally a lack of CWD in managed forests (Wikström and Eriksson 2000), and

increased knowledge of CWD should help environmental managers improve their management strategy of this important ecosystem resource.

CWD serves as an important habitat for many plants, as well as animals and micro-organisms (Graham 1925; Savely 1939; Triska and Cromack 1980; Harmon *et al.* 1986; Franklin *et al.* 1987; Maser *et al.* 1988; Spies and Cline 1988; Hansen *et al.* 1991; Keddy and Drummond 1996; Whiles and Grubaugh 1996; Eggleton *et al.* 1997; Sturtevant *et al.* 1997; Schowalter *et al.* 1998; Pyle and Brown 1999; Tainter and McMinn 1999; Grove and Meggs 2003; Debeljak 2006; McKenny *et al.* 2006; Stevenson *et al.* 2006). Coarse woody debris has also been identified as an important habitat for many threatened species (Berg *et al.* 1994; Ringvall *et al.* 2001). CWD are important stores of water, nutrients, and energy (McFee and Stone 1966; Grier 1978; Roskoski 1980; Spano *et al.* 1982; Boddy 1983a; Harmon *et al.* 1986; Franklin *et al.* 1987; Mattson *et al.* 1987; Maser *et al.* 1988; Spies and Cline 1988; Jurgensen *et al.* 1989; Means *et al.* 1992; Tinker and Knight 2001; Ganjegunte *et al.* 2004; Chojnacky and Heath 2002; Debeljak 2006; Bütler *et al.* 2007), but has received less attention than fine litter and roots (Idol *et al.* 2001). The water-holding capacity of CWD is especially important in dry or seasonally-dry environments (Harvey *et al.* 1979; Laiho and Prescott 1999).

1.1.1 EROSION MITIGATION

CWD serves an important role in erosion mitigation; reducing soil and nutrient loss from the ecosystem (Triska and Cromack 1980; Harmon *et al.* 1986; Gonor *et al.* 1988; Maser *et al.* 1988; Hodge and Peterken 1998; Laiho and Prescott 1999; Brown *et al.* 2003; Debeljak 2006; Bütler *et al.* 2007).

1.1.2 PROPORTION OF DETRITAL POOL

Coarse woody debris can form a large proportion of the detrital pool in forest ecosystems (Grier 1978). In a review of the literature, Woldendorp *et al.* (2002a) found that CWD generally accounted for more biomass than the combined mass of the fine litter and SDT pools in Australian forests where CWD, SDTs, and fine litter, were listed separately. CWD accounted for 65% of the total litter mass at these sites, with CWD accounting for the majority of the detrital mass in 13 of the 23 sites listed. Grier and Logan (1977) found, in a *Pseudotsuga menziesii* (Mirb.) Franco dominated conifer forest in the NW USA, that CWD accounted for 71% of the forest floor detrital mass, and that CWD and SDTs accounted for 81% of all detritus. The high loading of CWD

biomass makes it an important component of forests, especially in old-growth forests with their large trees and higher CWD loading (Spies and Cline 1988; Lindenmayer *et al.* 1999).

1.1.3 CARBON SEQUESTRATION

While carbon (C) is sequestered in CWD, it is released during the decomposition process (Woldendorp *et al.* 2002a); the C is initially incorporated into the bodies of the decomposer organisms and subsequently released to the atmosphere via respiration and death-and-decomposition of the decomposer organisms. Fire may also remove CWD mass by burning existing pieces of CWD (Van Lear 1996; Snowdon *et al.* 2000; Woldendorp *et al.* 2002a; Shang *et al.* 2004). The effects of fire are especially pertinent to eucalypt CWD, as the eucalypt forests and woodlands have evolved with fire as an important and necessary component of their ecology. Due to the large sizes of many Australian forest trees, which results in large amounts of CWD in eucalypt forest ecosystems (especially the large eucalypts growing in cool wet environments), it is important to account for the CWD mass when accounting carbon sequestered in Australian forests (Snowdon *et al.* 2000; Woldendorp *et al.* 2002a).

1.1.4 LONGEVITY OF CWD

Coarse woody debris provides some stability within an ever-changing environment. Due to the generally slow decomposition of CWD (Lambert *et al.* 1980; Triska and Cromack 1980; Graham and Cromack 1982; Silvester *et al.* 1982; Spano *et al.* 1982; Harmon *et al.* 1986; Chambers *et al.* 2000), the influence of an individual piece, if large in diameter, may last for hundreds of years (McFee and Stone 1966; Means *et al.* 1985; Franklin *et al.* 1987; Maser *et al.* 1988; Brown *et al.* 1998; Tainter and McMinn 1999). This longevity allows the CWD to provide a stable component within the dynamic forest ecosystem, and may give the resident CWD a 'pivotal' role in the overall dynamics of the ecosystem.

1.1.5 PAUCITY OF CWD STUDIES

Numerous authors have stated there have been relatively few studies on CWD (Fogel and Cromack 1977; Triska and Cromack 1980; Franklin *et al.* 1987; Spies *et al.* 1988; Schowalter 1992; Whiles and Grubaugh 1996; Feller 1997; Brown *et al.* 1998; Jonsson 2000; Chojnacky and Heath 2002; Eaton and Lawrence 2006; Bütler *et al.* 2007), with most studies of forest floor woody-debris decomposition focussing on fine litter and twigs (Harmon *et al.* 1986). The paucity of CWD studies is especially evident for the

tropics (Torres 1994; Delaney *et al.* 1998; Chambers *et al.* 2000). Coarse woody debris is possibly the least studied of the forest carbon pools (Harmon *et al.* 1986; Harmon and Hua 1991; Eaton and Lawrence 2006). However, there has been a recent interest shown in assessing the amount of CWD in the forest environment (Harmon *et al.* 1986; Ringvall *et al.* 2001), although the majority of these studies have tended to be in the United States and Canada in deciduous angiosperm and conifer forests (Woldendorp *et al.* 2002a). To date, there have been few studies of CWD in Australian forest ecosystems, especially old-growth forests (Chee 1999; Lindenmayer *et al.* 1999; Woldendorp *et al.* 2002a). Due to the slow decomposition of CWD, studies can take a long time to complete (Harmon *et al.* 1986), which undoubtedly is one reason for the paucity of CWD studies.

1.1.6 NEED FOR MORE RESEARCH/STUDIES

For effective management of the CWD pool, there is an urgent need for accurate information of CWD dynamics, and its role in forested ecosystems functioning with respect to stand health, ecosystem productivity, carbon- and nutrient-dynamics, and environmental change (Triska and Cromack 1980; Harmon *et al.* 1987; Keddy and Drummond 1996; Lee *et al.* 1997; Sturtevant *et al.* 1997; Schowalter *et al.* 1998; Chambers *et al.* 2000; Tietje *et al.* 2002; Debeljak 2006). The need for increased CWD research, to bridge knowledge gaps, is especially urgent for Australian forest ecosystems (Attiwill *et al.* 1996; Lindenmayer *et al.* 1999; Woldendorp *et al.* 2002a; Woldendorp and Keenan 2005; Yee *et al.* 2006).

1.2 WHAT IS CWD?

Coarse woody debris is woody debris found on the forest floor (e.g. Laiho and Prescott 1999), but is a separate component to litter. CWD is the coarser fraction, containing woody material and bark, with litter being the finer fraction, including all fallen plant components (Woldendorp *et al.* 2002a). CWD consists of woody material in the form of logs and large pieces of wood originating from tree stems and branches (Harmon *et al.* 1986; Brown *et al.* 1998; Pyle and Brown 1999; Shang *et al.* 2004). Litter is sometimes termed fine litter.

CWD and litter are distinguished by size, however, the threshold used to distinguish between them has not been standardised, and studies vary (Harmon *et al.* 1986; Woldendorp *et al.* 2002a). Due to differences in tree diameters in different ecosystems, the size threshold between CWD and litter is varied to match the prevailing size

distribution of CWD (Harmon and Sexton 1996) and the data requirements of the experiment (Woldendorp *et al.* 2002a).

Although many investigators have included standing dead trees (SDTs) as CWD in their surveys (e.g. Saldariaga *et al.* 1988; Spies and Cline 1988; Uhl and Kauffman 1990; Brown *et al.* 1998; Gale 2000; Woodall and Nagel 2006), it is common to ignore SDTs as they are usually measured in standing biomass surveys, along with the living trees (McKenzie *et al.* 2000). Many researchers whom do include SDTs in their CWD surveys separate the SDTs from the logs in their analyses (e.g. Spetich *et al.* 1999). In the literature, SDTs are often called 'snags' or 'stags'. 'Snag' is probably the most common term used in the literature, but is not used in this thesis to prevent confusion with aquatic CWD; which are often referred to as snags (Gonor *et al.* 1988). Idol *et al.* (2001) used the term down dead wood (DDW) to provide a subset of CWD where only the pieces lying prostrate on the ground are considered; this then excludes all standing dead trees. The rationale for ignoring standing dead biomass is that the prostrate component decomposes faster than the standing dead material, and consequently, has a greater affect on nutrient cycling (Idol *et al.* (2001). CWD also includes fallen branches and larger pieces of wood lying on the forest floor due to fragmentation of CWD and SDTs (Harmon *et al.* 1986). Coarse dead-roots have occasionally been classified as CWD (e.g. Pyle and Brown 1999; Shang *et al.* 2004), but these are usually considered to be a separate component from CWD.

In this thesis, CWD will refer to logs lying on the ground, or lying prostrate across other CWD, while standing dead trees will be referred to as SDTs.

Variations in the minimum size used to distinguish CWD from litter makes comparison between different studies difficult (Harmon *et al.* 1986; Woldendorp *et al.* 2002a). Harmon and Sexton (1996) recommended a minimum diameter of 10 cm for CWD. The 10cm minimum-diameter threshold has been used by many investigators (for a thorough discussion of CWD size thresholds see section 2.2.1; *Size Limits of CWD*). A minimum diameter of 7.5 cm has often been used in forest fuel inventories (Harmon and Sexton 1996; Woldendorp *et al.* 2002a; Brown *et al.* 2003); which corresponds to the 3" (imperial-measurement system) often used to classify "large woody fuel" (Brown *et al.* 2003). Occasionally, studies, especially those concerning forest fuel inventories, will set a maximum size for the CWD studied, ignoring large pieces of CWD. The reason for this is that the burning-time for large pieces of CWD is

slow, and the fuel studies are interested in the faster burning fractions of the fuel load (Woldendorp *et al.* 2002a).

1.2.1 CWD INPUT: FROM WHERE DOES CWD COME?

Tree mortality directly influences the amount of CWD (Harmon *et al.* 2000; Jönsson *et al.* 2007), as it is derived from living trees and branches that have died or been killed by disturbance. CWD is created when trees or parts of trees fall to the forest floor, because of death or breakage of living trees (Van Lear 1996). CWD can be generated naturally by wind, fire, disease, insect attack, natural thinning, land slippage, earchquake, drought, flooding, debris avalanches, collapse due to weight of snow or ice, excessive amounts of sunlight or heat, low temperatures, acid-rain, pollution, structural weakening due to decay, and death due poor competitiveness or old age (McFee and Stone 1966; Keller and Swanson 1979; Triska and Cromack 1980; Grier *et al.* 1981; Graham and Cromack 1982; Cooper 1983; Harmon *et al.* 1986; Franklin *et al.* 1987; Maser *et al.* 1988; Sedell *et al.* 1988; Spies and Cline 1988; Spies *et al.* 1988; Morrison and Raphael 1993; Keddy and Drummond 1996; Lee *et al.* 1997; Sturtevant *et al.* 1997; Anon 1998; Gale 2000; Gibbons *et al.* 2000; Clark *et al.* 2002; Currie and Nadelhoffer 2002; Tietje *et al.* 2002; Wermelinger *et al.* 2003; Shang *et al.* 2004; Debeljak 2006; Shifley *et al.* 2006; Garrett *et al.* 2007; Jönsson *et al.* 2007). The greater the number of causes-of-death in a forest stand, the greater the diversity in structural and functional roles provided by CWD in that particular stand (Maser *et al.* 1988).

High winds funnelling along creeks can also lead to tree knockdown on the outside of bends, where the wind tends to hit the forest from the side (Sedell *et al.* 1988). Flash floods travelling along creeks and rivers would have much the same impact, with tree knockdown occurring most notably on the outside of bends, but also along the edges of the creek; although much of the riparian vegetation uprooted would become aquatic CWD, as opposed to the CWD on the outside of the creek bend remaining as terrestrial CWD.

Commercial forestry operations, thinning and harvesting, are also major contributors to CWD formation in commercial forests. Anthropogenic CWD formation also exists in non-commercial forests, where trees are cleared for infrastructure, such as walking paths, clear viewing areas at lookouts, roads, parking areas, amenities buildings, and accommodation facilities. Many SDTs near walking paths and roads are also felled, as part of park/reserve management, if they are deemed to pose a risk due to a high probability of collapse.

CWD input rate from individual SDTs varies, depending on whether the whole SDT falls in a single event, or fragments slowly (Woldendorp *et al.* 2002a). The time lag between tree death and SDT fragmentation is influenced by cause of death, size, available microclimate for decomposer organisms, and species-specific toxins that repel decomposer organisms (Harmon *et al.* 1986). Death of standing trees may be caused by anthropogenic events, such as logging operations, or natural events as mentioned above (Harmon *et al.* 1986; Anon 1998; Tainter and McMinn 1999), and old age. Multiple tree-falls can generate large quantities of CWD (Greenberg 2001). Within a particular stand, CWD may exhibit a clumped, random, or uniform distribution, depending on the mode of tree death and fall (Harmon *et al.* 1986). Most multiple tree-falls are sporadic in nature (Tainter and McMinn 1999) and generate a pulse effect in CWD recruitment (Lambert *et al.* 1980; Franklin *et al.* 1987). As the spatial resolution changes from the individual stand scale to the forest or regional scale, CWD input would exhibit a clumped distribution, as the agents of tree mortality would not be distributed evenly over a forest at a regional scale (Harmon *et al.* 1986). The overall rate of CWD input, over a region, is primarily influenced by the productivity of the forest, and secondarily by the size distribution of the trees in the forest (Harmon *et al.* 1986). (The rate of CWD input is primarily influenced by the amount of wood in the living trees. The greater the number or trees and the larger the trees, for a given area, the more wood will be transferred into the CWD pool when the trees die and fall.)

1.2.2 WHAT INFLUENCES CWD FORMATION?

The amount of CWD is influenced by stand disturbance (Hély *et al.* 2000; Keith *et al.* 2000; Woldendorp *et al.* 2002a). CWD volume generally increases during and soon after disturbance, but then declines because of the decomposition of the resultant CWD and the low initial CWD addition rate of the regenerating stand, CWD volume then increases again as the stand matures; due to increasing tree mortality (Hély *et al.* 2000). CWD amounts in young stands are greatly influenced by stand history, due to the low input rate of young stands, and the proportionately high loading of resident CWD from the previous stand (Spies *et al.* 1988; Lindenmayer *et al.* 1999). Due to the slow decomposition rates of large CWD pieces, even old-growth forests can contain CWD from previous stands (Woldendorp *et al.* 2002a). Grier (1978) found that 36% of CWD in a 121-year-old mixed-conifer forest was from the previous stand (76 Mg ha^{-1} out of 211.7 Mg ha^{-1}).

CWD volumes are dependent upon stand age, species, density, productivity, tree size, and climate (Harmon *et al.* 1986; Keith *et al.* 2000; Woldendorp *et al.* 2002a). Management practices also influence CWD volume within forests (Keith *et al.* 2000; Woldendorp *et al.* 2002a). Logging reduces standing biomass, but the residue tends to increase CWD mass (Woldendorp *et al.* 2002a). CWD volumes are also dependent upon fire; as fire will reduce the CWD on the forest floor through burning, but then increase the short-term recruitment rate of CWD due to tree death in the fire (Franklin *et al.* 1987; Woldendorp *et al.* 2002a; Debeljak 2006). Morrison and Raphael (1993) found that trees killed by fire fell sooner than SDTs untouched by fire. The initial-reduction-then-increase in CWD amounts is caused by the fire-killed trees becoming SDTs during the fire, and then falling as CWD some time after the fire (Spies and Cline 1988).

Charred logs have a reduced decay rate (USDA Forest Service 2001), however, the initial fire causes a pulse of mass-loss, albeit the extent will depend on the intensity of the fire, the moisture-content of the log, and the diameter of the log (larger-diameter logs will lose proportionally less mass than smaller-diameter logs). The greater the intensity of the fire, the greater the proportion of the log that will be lost in the fire, but the greater the moisture-loss and sterilisation of the log, resulting in a greater reduction in decay, at least in the short-term; which may, or may not, result in a long-term overall increase or decrease of decay rate.

1.3 ENVIRONMENTAL ROLES OF COARSE WOODY DEBRIS

Coarse woody debris plays an important role in ecosystem functioning, it is an important storehouse of nutrients and water, an important habitat for many organisms, and increases the structural complexity of the forest (Lambert *et al.* 1980; Grier *et al.* 1981; Abbott and Crossley 1982; Spano *et al.* 1982; Jurgensen *et al.* 1984, 1987; Harmon *et al.* 1986, 1987; Franklin *et al.* 1987; Mattson *et al.* 1987; Spies and Cline 1988; Spies *et al.* 1988; Hansen *et al.* 1991; Sturtevant *et al.* 1997; Schowalter *et al.* 1998; Næsset 1999a, Pyle and Brown 1999; Greenberg 2001; Woldendorp *et al.* 2002a; Chojnacky and Heath 2002; Bütler *et al.* 2007; Jönsson *et al.* 2007). The functional importance of CWD depends on quantities, size distribution, decay stage, species specific chemical constituents, spatial distribution, mode-of-death, and whether it is prostrate or elevated (Harmon *et al.* 1986; Franklin *et al.* 1987). Due to heterogeneity of decay within a single log, individual logs may be more important for species richness and diversity than is suggested by classifying a log into a single decay class (Pyle and

Brown 1999). CWD recruitment not only creates opportunity for decomposer organisms, it allows light to penetrate to the forest floor providing opportunities for successional colonising-species (Maser *et al.* 1988). With a large resident decomposer-community, a log may contain a greater proportion of living biomass than existed in the living tree (Franklin *et al.* 1987).

Energy is required by biological systems for growth and regeneration. As CWD is a storehouse of energy, it is an important element in the energy flow of forest ecosystems (Chojnacky and Heath 2002).

The ability of CWD to store water, providing a moist environment for lengthy periods, maintains a high species richness and diversity of the decomposer community during dry spells. This maintains a higher decomposition rate than otherwise might be expected (Brown *et al.* 1996). Besides storing water internally, CWD maintains higher moisture levels in the soil immediately beneath, providing a refuge for tree seedlings that have not yet developed a deep root system (Abbott and Crossley 1982). Many invertebrates use CWD for shelter and feeding sites (Torres 1994; Brown *et al.* 2003). Grove and Meggs (2003) found that CWD offered protection for beetles escaping fire in *Eucalyptus obliqua* L'Hér. forests in southern Tasmania. Skinks in the eucalypt woodland of tropical Australia have been observed (*pers obs.*) using the shade of CWD as thermoregulation-sites, as well as ambush-sites (e.g. ambushing passing spiders).

1.3.1 HABITAT ROLE

Many organisms are dependent on CWD for habitat (Meggs 1996; Schowalter *et al.* 1998; Lindenmayer *et al.* 1999; Pyle and Brown 1999). The comparatively-stable environment within CWD provides some measure of protection from frost in cold environments (Whiles and Grubaugh 1996), and its role of buffering against environmental extremes makes it an important refugia for associated animals (Grove and Meggs 2003). As CWD progresses through the decay process, it provides a progression of different habitats (Savely 1939; Pyle and Brown 1999), hosting a succession of different resident organisms (Graham 1925). Often a species can only inhabit a log after it has been pre-conditioned by a predecessor-species; some insects eat fungal hyphae in the wood, showing that the wood must first be colonised by the relevant fungi before being colonised by these insect species (Graham 1925; Savely 1939). Large-diameter CWD, due to slower decomposition, provides long-lasting habitats (Maser *et al.* 1988). Due to the diversity of habitats that exist within a log at any time, a single log can be considered a single ecological-unit (an isolated

homogeneous matrix that contains a community of interacting organisms) that exists within a larger ecosystem (Graham 1925).

1.3.1.1 Plant Habitat

Coarse woody debris lying of the forest floor can be an important habitat for other plants (Harmon *et al.* 1986; Söderström 1988; Pyle and Brown 1999; Tainter and McMinn 1999), especially for seedling establishment (McCullough 1948; Triska and Cromack 1980; Graham and Cromack 1982; Sollins 1982; Maser *et al.* 1988; Spies and Cline 1988; Harmon 1989; Harmon and Franklin 1989; Keddy and Drummond 1996; Hodge and Peterken 1998; McKenny and Kirkpatrick 1999; Bütler *et al.* 2007); either as a nurse log hosting seedlings epiphytically or due to the log's role in trapping loose soil (see 1.1.1 *Erosion Mitigation*). Spies and Cline (1988) found seedlings grow preferentially in the moister soil beneath CWD. CWD provides seedlings with some measure of protection from trampling by animals (Brown *et al.* 2003). CWD also provides habitat for epiphytic plants that prefer the low-light environment near the forest floor, such as bryophytes and some ferns (Ashton 1986); Cain and Sharp (1938) termed organisms that used CWD, but not living wood, as epixylic.

1.3.1.2 Animal Habitat

CWD has been identified as an important habitat for fauna (Spies and Cline 1988; Hodge and Peterken 1998; Pyle and Brown 1999; Tainter and McMinn 1999; Stevenson *et al.* 2006), including insects and other invertebrates as well as vertebrates (Savely 1939; Triska and Cromack 1980; Harmon *et al.* 1986, 1987; Torres 1994; Meggs 1996; Whiles and Grubaugh 1996; Eggleton *et al.* 1997; Sturtevant *et al.* 1997; Grove 2002; Grove *et al.* 2002; Grove and Bashford 2003; Jansen *et al.* 2003; McElhinny 2005; McElhinny *et al.* 2006a, b; McKenny *et al.* 2006; Garden *et al.* 2007). CWD not only provides a shelter-site from predators, but also affords a sheltered feeding site for animals that feed on CWD-inhabiting invertebrates (Whiles and Grubaugh 1996). Whilst there is a relatively large amount of literature regarding the insect and fungal usage of CWD, very little of this attempts to address the issues of volume (m^3 ha^{-1}), condition, and distribution (i.e. discontinuity) at the landscape level (Greenberg 2001). Papers addressing these issues are extremely rare for other groups of organisms. *Nothofagus cunninghamii* (Hook.) Oerst. CWD was observed, in southern Tasmania, with the upper portion stripped away by parrots searching for insect larvae (*pers obs.*).

1.3.1.3 Fungus (inc. Lichen) and Micro-organism Habitat

CWD is an important habitat for many species of fungi and micro-organisms (Abbott and Crossley 1982; Meggs 1996; Lindenmayer *et al.* 1999; Tainter and McMinn 1999), many of which are involved in the breakdown of the CWD. CWD is also an important habitat for many microarthropods (Christensen 1977; Abbott and Crossley 1982), many of which inoculate the CWD with decomposer micro-organisms and fungal spores, which directly affect the decomposition rate of the CWD (Abbott and Crossley 1982).

1.3.2 NUTRIENT CYCLING

During decomposition, the nutrients sequestered in CWD are recycled back to the soil, enhancing soil fertility (Fogel and Cromack 1977; Harmon *et al.* 1986; Maser *et al.* 1988). The decomposition of CWD plays a prominent role in site productivity, through its affect on the quantity, and quality, of soil organic matter (Jurgensen *et al.* 1997). CWD may contain a large portion of a forest's nutrients, and the productivity of a forest is likely to be influenced by the slow return of these nutrients to the soil (Brown *et al.* 1996; Ganjegunte *et al.* 2004), as shown by Grier (1978) and Lang and Forman (1978). CWD can thus act as a slow release fertiliser for the forest ecosystem (Triska and Cromack 1980; Barber and Van Lear 1984; Maser *et al.* 1988). The nutrients released by decaying CWD provide heterogeneity of nutrient concentrations in the ecosystem, with higher concentrations found beneath the CWD (Schowalter 1992; Schowalter *et al.* 1998). The ability of CWD to act as a nutrient sink, slowly releasing nutrients to the system, helps reduce potential losses of nutrients from the forest system (Abbott and Crossley 1982). Larger-diameter logs provide a reserve of longer-lasting nutrient stores than do smaller-diameter logs (Spetich *et al.* 1999).

1.4 THE ROLE OF CWD IN CARBON SEQUESTRATION

Carbon concentration of CWD generally remains stable during decomposition, as found by Harmon *et al.* (1987; conifer), Torres (1994; angiosperm), Chee (1999; conifer and angiosperm), Rose (2000; conifer), Currie and Nadelhoffer (2002; conifer and angiosperm) and Bütler *et al.* (2007; conifer). However, Means *et al.* (1992), in a study of *P. menziesii* (a conifer), found C concentration decreasing during decomposition.

In the literature, percentage C concentrations range from a maximum of 55.2% (Currie and Nadelhoffer 2002; mixed angiosperm) to a minimum of 42.9% (Idol *et al.* 2001; mixed angiosperm). Actual C concentrations range from a maximum of 0.298 g

cm^{-3} (Currie and Nadelhoffer 2002; mixed angiosperm* to a minimum of 0.059 g cm^{-3} (Alban and Pastor 1993; *Populus tremuloides* Michx. angiosperm†; — calculated from percent of wood density provided).

Only relatively recently has global warming and the greenhouse issue become a concern (Anon 1998). There are many 'greenhouse gases', but the three most important gases reputedly being increased by anthropogenic activities are carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O), and these have increased considerably since the middle of the 18th century due to industrialism (IPCC 1995, 1997a). Greenhouse gases restrict the radiation of infrared energy out of the Earths atmosphere into space, while restricting incoming infrared radiation to a much lesser extent, resulting in a net increase in the Earths environmental temperature (IPCC 1997b). Of these gases, CO_2 is thought to have the greatest affect on global warming (IPCC 1997a); whilst, on a molecule-to-molecule basis, CH_4 is a greater contributor to global warming than is CO_2‡, the atmospheric concentration of CH_4 has stabilised since 1999 (Bousquet *et al.* 2006), and does not pose the threat that increasing CO_2 poses to global climate change.

1.4.1 CARBON DIOXIDE

Of these three most-important greenhouse gases, this project is concerned with CO_2. Carbon dioxide emissions from the burning of fossil fuels and deforestation are causing an increase in the atmospheric carbon dioxide concentration, which, due to an enhanced greenhouse effect, is predicted to result in long-term global climate change (Houghton *et al.* 1983; IPCC 1995).

Atmospheric carbon dioxide concentrations have been increasing since global deforestation began in Europe before the middle ages, and has increased further during the last 100 years due to increased burning of fossil fuels (Sedjo 1992; Karjalainen 1996). Atmospheric CO_2 concentrations increased by 29% from 280 parts per billion by volume (ppbv) in 1750 to 360 ppbv in 1992 (IPCC 1995). Initially, it was the higher latitudes that experienced the most deforestation, but this changed to the lower latitudes during the 20th century (Karjalainen 1996). Dixon *et al.* (1994) claim that 1.65 Pg C yr^{-1} is released to the atmosphere because of land use change in the tropics.

Through photosynthesis, C is sequestered from the atmosphere by plants. However, photosynthesis is not constant, and rarely reaches a potential maximum, due to the

Footnotes
* Calculated from percent of wood density provided.
† Calculated from percent of wood density provided.
‡ Methane (CH_4) contributes about 8.4 times CO_2 on a molecule-to-molecule basis.

limitations imposed by the prevailing climate, local topography, soil nutrient fertility, size and age structure of individual forests, and is influenced by differences in photosynthetic efficiency between different species (Anon 1998). Through the actions of photosynthesis, plant material is a store of C, and CWD has the potential to be a large store of C in environments that contain large quantities of CWD.

1.4.2 THE NEED FOR CARBON SEQUESTRATION

The threat of climatic upheaval, due to increasing concentrations of atmospheric greenhouse gases, has inspired many nations to look for means to mitigate, or even reverse, the trend of increasing greenhouse gas concentrations (Chojnacky and Heath 2002). Recently, policy makers have become interested in the potential for forest and woodland ecosystems as potential storehouses of carbon (Eamus *et al.* 2000).

1.4.2.1 Carbon Sinks

Biomass accumulation of global forests may be a means of offsetting the increasing concentration of atmospheric CO_2 (Brown *et al.* 1992; Lugo and Brown 1992; Kauppi *et al.* 1992; Sampson *et al.* 1993; Dixon *et al.* 1994). Dixon *et al.* (1994) concluded that high and mid latitude forests sequester 740 ± 190 Tg C yr^{-1} due to growth within existing forests and aforestation, forming major carbon sinks.

Approximately 50% of forest vegetative biomass is carbon (Anon 1998). Unfortunately, the estimated sequestration of C by high and mid latitude forests (740 Tg C yr^{-1}) is less than half the estimated release of C by the low latitude forests (1.65 ± 0.4 Pg C yr^{-1}) (Dixon *et al.* 1994), which shows a net release of approximately 900 ± 400 Tg C yr^{-1} from forests globally (Dixon *et al.* 1994).

1.4.2.2 CWD as a Carbon Reservoir

Dead organic debris on the forest floor is a carbon reservoir (Harmon and Hua 1991; Hodge and Peterken 1998; Næsset 1999a; Keith *et al.* 2000). Woody debris, due to its slow decomposition compared to non-woody debris, represents a potential long-term store of C (Jurgensen *et al.* 1989; Harmon and Hua 1991; Schowalter 1992; Brown *et al.* 1996; Schowalter *et al.* 1998). If decomposition rates, per given area of forest, are slower than the biomass accumulation rates of the growing, or regenerating, forest, the forest becomes a carbon sink (Lugo and Brown 1992).

It is convenient to divide the stored C within forest ecosystems into pools that are measured separately (Anon 1998). As most of a tree's biomass is stored aboveground

(Tajchman *et al.* 1996), CWD derived from a tree's aboveground parts is an important form of sequestered carbon (Lang and Forman 1978; Schowalter 1992; Chojnacky and Heath 2002; Waddell 2002). CWD has been largely neglected with respect to C sequestration (Eaton and Lawrence 2006), especially in studies of Australian forests (Woldendorp *et al.* 2002a), despite being a major component of a forest's C storage (Graham and Cromack 1982; Mattson *et al.* 1987; Harmon *et al.* 1990; Lugo and Brown 1992; Schowalter 1992; Torres 1994; Delaney *et al.* 1998; Gale 2000; Ganjegunte *et al.* 2004; Bütler *et al.* 2007).

The retention of slow-decomposing material is important for forests when being considered for roles in C sequestration. CWD is the slowest decomposing material in the manageable forest C pools; roots often decay slower, but are not as easy to manage as CWD. The decay-dynamics of CWD may determine whether a forest region is a C-source or C-sink (Chambers *et al.* 2000). Consequently, it is important to account for CWD and its decomposition when accounting for net ecosystem exchange of C in forest environments (Keller *et al.* 2004a; Eaton and Lawrence 2006), as the omission of CWD in global C budgets has caused an underestimation of the C pool in forest ecosystems (Delaney *et al.* 1998).

Nabuurs and Mohren (1995) stated that evergreen forests might contain the largest long-term stock of carbon in biomass. This is obviously due to their year round growth patterns. The higher biomass stock in living trees would also lead to a higher biomass stocking in CWD.

1.5 AIMS AND OBJECTIVES OF PROJECT

This project has been designed to address some of the many knowledge-gaps concerning eucalypt CWD dynamics, and the paucity of information required by ecosystem managers to manage the CWD pool within native ecosystem. To most-effectively address the issue of how variable are Australia's ecosystems with respect to CWD dynamics, it was decided that a project working along a latitudinal gradient would be most useful, encompassing the range from far north Queensland (tropical) to southern Tasmania (cool temperate). One of the necessary tools was the development of a eucalypt-specific decay-classification system, as previously decay-classification systems had been modifications of systems used for Northern Hemisphere studies. Knowledge-gaps that have been addressed are the decomposition dynamics of Australian CWD, the amount of CWD in native forest environments, and the carbon sequestered and released by native forest ecosystems.

The formal hypotheses being tested in this project component of this thesis are:

Is there a difference in CWD volumes and mass, per area, at the different areas surveyed?

Are the decay rates at the different areas different from each other?

Do the different forest types emit the same amount of carbon as each other?

Is there a latitudinal effect on decomposition rates?

The relative locations of the sampling regions can be seen in Map 1-1.

The aims of this study are:

Measure the amount of CWD (volume and mass) in two temperate wet eucalypt forests (southern New South Wales and southern Tasmania), dry eucalypt woodland (central Queensland), and tropical rainforest (northern Queensland),

Calculate decay rates of CWD for each area,

Calculate C release from the CWD of each area on a per area basis per year,

Devise a decay class system for eucalypts based on cluster analysis.

Recommend actions to improve CWD management strategies with respect to its role in ecosystem functioning.

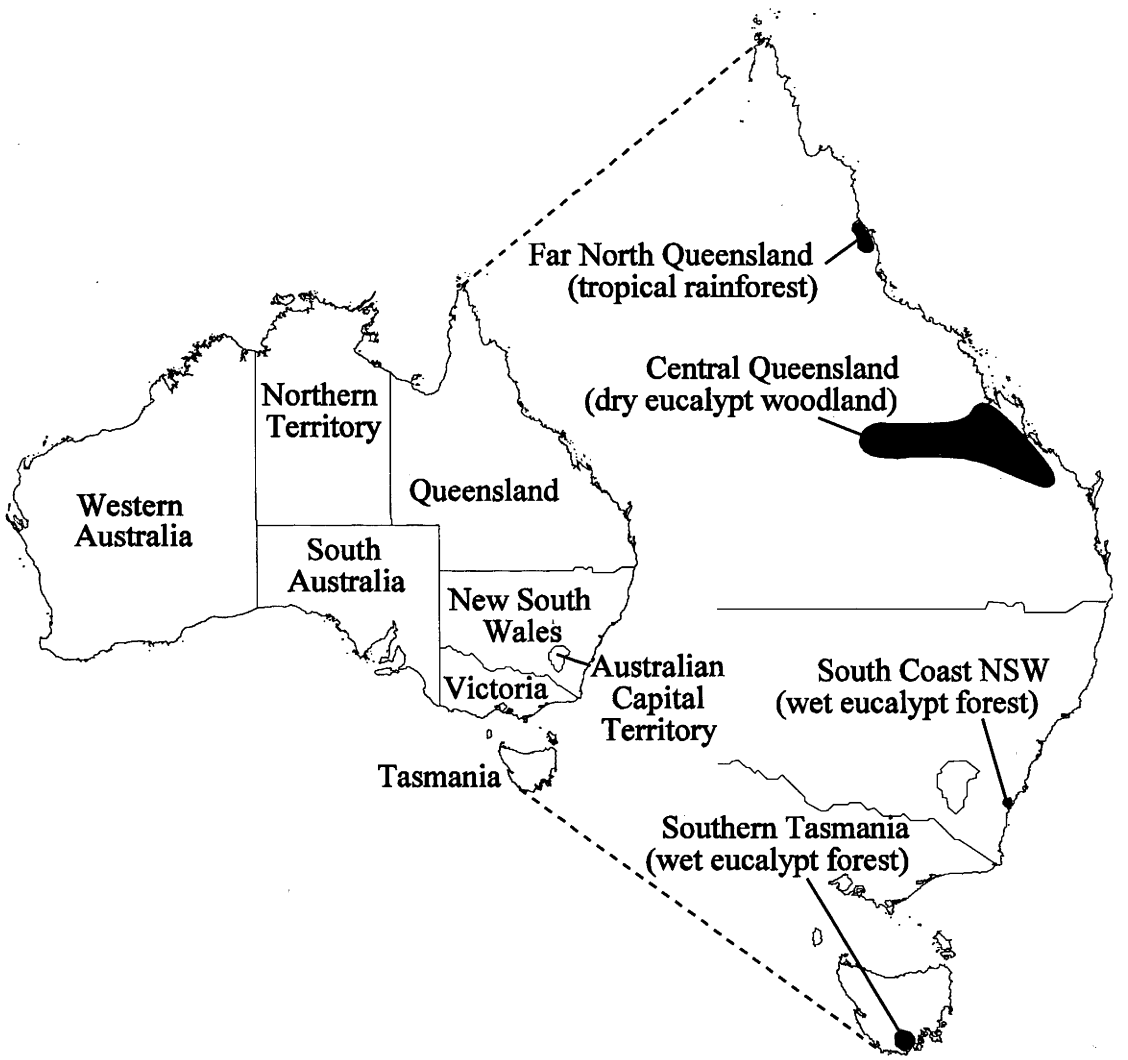
Note, in the literature, wet eucalypt forests are often referred to as "wet sclerophyll forests" (Beadle and Costin 1952)

1.6 THESIS OUTLINE

This thesis is structured with a review of the literature in Chapter 2, which includes a comparative appraisal of the different methods used to survey CWD, and the processing of CWD samples. Chapter 3 lists the methods used to sample and process the CWD studied in this project, and the analyses methods used. The results follow in Chapter 4. Chapter 5 is a discussion of the results of the project in isolation and with comparison to the literature (as previously discussed in the literature review chapter), and a discussion of the implications upon CWD management as affected by the CWD decay rates. The conclusions are in Chapter 6. There are several appendices at the end of the thesis, and these were necessary to explain further the philosophy behind some of the methods used.

Some studies of Australian CWD use the terminology of the Specht system of forest classification (e.g. Woldendorp 2000; Woldendorp *et al.* 2002a, b, 2004; Woldendorp

and Keenan 2005). Under the Specht-system (Specht 1970) of vegetation-type classification, the southern Tasmanian forest sites are described as "tall open-forest", south-coastal NSW as "open-forest", central Queensland as "open-woodland", and far north Queensland as "closed-forest". In this thesis, the sampling sites are described as 'wet eucalypt forest' for southern Tasmanian and south-coastal NSW, 'dry eucalypt woodland' for central Queensland, and 'tropical rainforest' for far north Queensland. Non-Specht descriptions are used in this thesis, as they are more informative to readers unfamiliar with Australian biomes.



Map 1-1. Map of eastern Australia showing the boundaries of the four sampling areas. All areas are eucalypt dominated except for the tropical rainforest of Far North Queensland.

CHAPTER 2

LITERATURE REVIEW

2.1 GENERAL REVIEW OF LITERATURE

As coarse woody debris (CWD; logs lying on the forest floor) decays, it progresses from the solid wood of the living tree to inconspicuous widely-dispersed components (Pyle and Brown 1999). The woody material of CWD lost through decay can be in the form of gaseous emissions to the atmosphere, as well as liquefied and solid matter that is transported into the soil (Jenny *et al.* 1949), but some of the woody material will be incorporated into the biomass of the decomposer organisms.

The CWD-literature is very heterogeneous, reflecting the complexity of its contribution to ecosystem functioning, with different authors tending to focus on specific aspects of the amount, role, and function, of CWD in specific environments. This has led to CWD-research being broad-scoped, with many isolated sub-disciplines within the context of CWD-research; the isolated research-areas, or sub-disciplines, belie the true nature of the interactions that take place within the context of CWD-dynamics. This literature review has deliberately been made comprehensive in order to provide a general overview of the literature, as well as placing the research of this project in context as belonging to the decay-dynamics sub-discipline of CWD-research. In this chapter, the review of the literature will firstly focus on the general importance of CWD and processes of decay. This review will also concentrate on the factors that promote and inhibit decay. Secondly, the review will cover the importance of the decaying material, particularly the role of nutrient recycling. There is a comprehensive review of nitrogen-dynamics in CWD, accompanied by a brief review of the other commonly-studied nutrients. Finally, there is a comprehensive review of the methods used to measure both CWD amounts and decay, including both field and laboratory-based studies. This last section also includes an appraisal of commonly-used decay models.

2.1.1 DECOMPOSITION OF CWD

Interest in the decomposition dynamics of CWD has increased in recent decades (Sinsabaugh *et al.* 1992). The understanding of CWD decomposition is essential for the effective management of native forests, and this requirement is just as pertinent for the management of native eucalypt forests in Australia (Attiwill *et al.* 1996).

2.1.1.1 What is Decomposition

Within a forest ecosystem, dead organic matter on the forest floor is subjected to fragmentation by structural breakdown, and to decomposition by decomposer organisms (Minderman 1968; Tainter and McMinn 1999; Woldendorp *et al.* 2002a). CWD decomposition is an intricate process (Brown *et al.* 1998) which includes leaching of non-structural compounds, mineralisation by micro-organisms, and physical breakdown (Brown *et al.* 1996). Decomposition is influenced by the substrate characteristics of the CWD, as well as the environmental conditions under which the decay is occurring (Moorhead *et al.* 1996). CWD, and other woody litter on the forest floor, has a markedly slower decomposition rate than leaf litter (Maser *et al.* 1988).

Decomposition of the physical structure of CWD is a result of the chemical degradation of the structural compounds that form the supportive matrix into simple inorganic molecules (Moorhead *et al.* 1996), which can be readily absorbed by living plants. This breakdown of complex structural molecules into simpler non-structural inorganic molecules is done by micro-organisms. The loss of biomass due to physical breakage, by the exertion of a physical force on the CWD, is not decomposition. (That is, the shattering of pieces of CWD due to the impact force exerted on the CWD when it hits the ground, because of kinetic energy, is not decomposition.) Decomposition of CWD is a slow process, and can take many years to complete (Swift *et al.* 1976; Swift 1977; Lugo and Brown 1992).

IMPORTANCE OF DECOMPOSITION

Although the growing forest sequesters C, helping to mitigate the global increase in greenhouse gases, some of this C is released back into the atmosphere as CO_2 through decomposer respiration and the decay of forest floor litter and soil organic matter (Karjalainen 1996; Mackensen and Bauhus 1999). Temnuhin (1996) measured an average CO_2 emission rate of 1.7 kg ha^{-1} day^{-1} from the decomposer fungi inhabiting a Russian forest with a CWD loading of 11.3 m^3 ha^{-1}; which equates to a CWD fungal-respiration-rate of 150 g CO_2 m^{-3} CWD day^{-1} (0.150 kg CO_2 m^{-3} CWD day^{-1}). (The 159 year old forest consisted of 90% conifer and 10% deciduous angiosperm species.) The emission rate was considered low by the author, although it must be said that the CWD loading was also low. The emissions measured were from the intermediate decay states (classes II, III, and IV), as no class-I or class-V CWD was present. Temnuhin (1996) claim that CO_2 release from CWD of old-growth ("virgin") forests may match that of the soil.

During decomposition, some of the forest C is assimilated into the soil (Woldendorp *et al.* 2002a), and some is assimilated into the decomposer organisms (providing growth). Unfortunately, the decomposition of woody debris has received relatively little attention compared to that of the finer litter component of the forest floor (Grier 1978; Harmon *et al.* 1986). Further work on the decomposition of woody material is urgently required for effective management of the CWD pool (Brown *et al.* 1996).

Arthur *et al.* (1993) found that root mass within CWD increases significantly during the decomposition of CWD. They postulated that this was the result of release of the majority of nutrients during the latter stages of decomposition, along with its increased water holding capacity. This proves the importance of CWD to the growing forest, additional to its ability to sequester C. Decay of CWD, and other litter, is important to the nutrient cycling of forest ecosystems (Melillo *et al.* 1982), as it controls the availability of nutrients to living trees (Moorhead *et al.* 1996), and consequently, controls forest productivity. Decomposition of wood that has been incorporated into the soil is also important in maintaining forest productivity (Swift 1977; Larsen *et al.* 1978).

Moorhead *et al.* (1996) states "decomposition is comparable in importance to primary production as a fundamental ecosystem process". To assess the influence of CWD on ecosystem functions and productivity accurately, additional knowledge of CWD decomposition dynamics is essential (Wieder and Lang 1982; Erickson *et al.* 1985).

2.1.1.2 Decomposition Processes

FRAGMENTATION (WEATHERING) AND LEACHING (CHEMICAL EROSION)

It is suggested that the freezing of water contained within the CWD of temperate forests would lead to fragmentation (weathering) of the CWD; Garrett *et al.* (2007) describe CWD weathering as "the physical and chemical breakdown of wood due to climatic elements". An increase in the incidence of fragmentation would lead to increase in the breakdown of structural molecules and leaching of non-structural molecules, due to the effect of increasing the surface-area-to-volume ratio of the CWD (Brown *et al.* 1996); galleries created by boring invertebrates also facilitate the penetration of water into CWD, enhancing leaching (Torres 1994). The breakdown of complex organic molecules to simple inorganic molecules, by decomposer micro-organisms, results in the leaching of these simpler molecules to the surrounding environment (Brown *et al.* 1996).

This gives a two-phase character to the leaching of CWD material during decomposition. Initially, the leaching occurring in CWD is of the non-structural molecules, but this is replaced by the leaching of simple molecules released by the degradation of complex structural molecules.

Carbohydrates are water-soluble (Ganjegunte *et al.* 2004), and some of the reduction in carbohydrate concentration found in CWD would be due to leaching; although how important leaching of carbohydrates is when compared to biotic-removal by decomposer organisms is unclear. Leaching of tannins and phenols from CWD, which inhibit fungal growth in wood, decrease resistance to decay (Scheffer 1957; Cameron and LaPoint 1978; Baker *et al.* 1983). The physical removal of basidiocarps ("mushrooms") from logs is another means of nutrient-export from CWD (Schowalter *et al.* 1998). CWD has lower nutrient concentrations than living trees (Ashton 1975; Means *et al.* 1992) due to the breakdown and removal of residual nutrients.

2.1.1.3 Controlling Factors of Decomposition

There are many complex and interacting factors that affect the rate of decomposition of CWD (Næsset 1999b). Decomposition rates of CWD are influenced by the species-specific chemical properties of the wood in respect to nutrients and toxins, as well as diameter and density of the CWD piece, the metabolic efficiency of the decomposer organisms present, and the prevailing climate and the affects it has on the CWD microclimate affecting the decomposer organisms (Daubenmire and Prusso 1963; Meentemeyer 1978; Melillo *et al.* 1982; Erickson *et al.* 1985; Currie and Nadelhoffer 2002; Eaton and Lawrence 2006). CWD decomposition rates are affected by climate via the affect the moisture and temperature régime has on the decomposer organisms directly, and indirectly through the leaching of nutrients and toxins (Scheffer 1957; Abbott and Crossley 1982; Melillo *et al.* 1982; Boddy and Swift 1984; Brown *et al.* 1996; Chambers *et al.* 2000; Ganjegunte *et al.* 2004).

MOISTURE AND TEMPERATURE AFFECTS ON DECAY RATE.

Climate can have a large affect on CWD decay (Söderström 1988; Currie and Nadelhoffer 2002), especially the temperature and moisture régime (Grier 1978; Spies and Cline 1988; Delaney *et al.* 1998; Hicks *et al.* 2003). Microclimate influences decay rate directly, as well as indirectly through the selection of appropriately-adapted decomposer organisms (Griffith and Boddy 1991a).

MOISTURE. Available moisture is a major factor in determining decomposition rates of CWD (Ausmus 1977; Abbott and Crossley 1982; Erickson *et al.* 1985; Spies and Cline 1988; Moorhead *et al.* 1996; Pyle and Brown 1999). Decaying-wood holds more water than living-wood (Savely 1939). This water is derived from the replacement of decomposed structural material from water contained in rain and fog (Erickson *et al.* 1985), as well as from metabolic water (Boddy 1983b) liberated by fungal degradation of structural material (Griffin 1977).

Moisture content of CWD increases during decomposition (Meredith 1960; Yoneda 1975; Lambert *et al.* 1980; Roskoski 1980; Bütler *et al.* 2007) due to an increase in void-space (Savely 1939; Yoneda 1975; Boddy 1983a), and then stabilises (Maser *et al.* 1988). After the moisture-level stabilises, it may decrease toward the end of the decay process due to the void-space becoming too large to maintain adsorption against the 'pull' of gravity (Boddy 1983a; Griffith and Boddy 1991a). As decomposition proceeds, and void-space increases, the CWD piece absorbs and desorbs water faster, as there is less restriction to water movement within the wood matrix (Boddy 1983a; Griffith and Boddy 1991a).

As moisture availability increases, the decomposition rate increases (Meentemeyer 1978; Erickson *et al.* 1985; Edmonds *et al.* 1986; Schowalter 1992; Hély *et al.* 2000). Hendrickson (1991) postulated that the ability of N_2-fixing bacteria to fix atmospheric N_2 is probably controlled by moisture availability to some extent. Indeed, Hicks *et al.* (2003) found that moisture did have a significant influence on the ability of N_2-fixing bacteria to fix N_2, which in turn has an affect on decay rate; the higher the moisture level, the greater the rate of N_2-fixation, and the higher the decomposition rate (see 2.1.4.1 for a discussion of this point).

However, Moorhead *et al.* (1996) suggests the existence of an optimal moisture concentration for decomposer micro-organism efficiency for fine litter in soil. They suggest that saturated soils inhibit decay rates due to anaerobic conditions. This is unlikely to occur as often in CWD, as water can easily drain away from the CWD pieces, unless they are in areas that are regularly submerged, such as floodplains. However, water trapped within CWD located in moist environments may become slightly anaerobic due to decomposer organism respiration, but probably not to the extent of saturated soil. High moisture availability is more likely to enhance CWD decomposition than it is to retard it.

Erickson *et al.* (1985) found that as available moisture decreased the decomposition rate for the conifer *Pinus ponderosa* decreased. This pattern was repeated for Edmonds *et al.* (1986) studying *P. menziesii*, also a conifer. However, Edmonds *et al.* (1986) found that moisture content was not correlated to the decomposition rate for the angiosperm *Alnus rubra* Bong.

Atmospheric relative-humidity (humidity) also has an affect on CWD decomposition, with lower-humidity environments having a slower rate-of-decay (Gale 2000), as lowered-moisture levels lead to decreased microbial and fungal activity (Griffith and Boddy 1991b; Evans *et al.* 1998). Lower atmospheric humidity affects CWD decomposition as moisture moves from the log to the atmosphere. The moisture régime within a log has a determining effect on the species composition of the decomposer organism community, and consequently, the successional dynamics of the decomposition process (Griffith and Boddy 1990). Higher moisture-levels in a log will allow the log to support a greater species richness and diversity (Graham 1925; Savely 1939). However, very high near-saturation moisture levels can create adverse conditions that reduce species richness and diversity of log-inhabiting species (Graham 1925).

Hély *et al.* (2000) claim that forests in drier climates would have a greater accumulation of CWD due to slower decomposition rates. This was claimed to be a result of the inauspicious conditions for the decomposer fungi. The problem with this statement is that drier climates usually have smaller and slower-growing vegetation, which puts down less CWD per area per year; this counteracts the slower decomposition rate to some degree. Consequently, drier climates do not necessarily result in greater accumulations of CWD.

Meentemeyer (1978) stated that actual evapotranspiration (AET) "correlates well with decay rates". However, Meentemeyers' study only tested AET against lignin content for their predictive values of decay rates, and was concerned with leaf litter only, not coarse litter. Additionally, Meentemeyer (1978) estimated the AET; using water budgeting methods. Evapotranspiration is the loss of moisture from the soil through evaporation and transpiration. Since leaf litter is directly affected by soil moisture, as it is in direct contact with the soil, then AET would be expected to have a major affect on the decomposition rate of leaf litter. However, CWD often has a higher moisture content than the soil it is contacting, and often has sustained high moisture contents into dry periods, when the soil has dried out. Consequently, it is unlikely that

AET would be a good predictor of CWD decomposition rates, especially for larger pieces of CWD. Even for leaf litter, AET is not always a good predictor of decay rates, especially in environments with high or low AET (Whitford *et al.* 1981). Although Meentemeyer (1978) correlated AET with leaf-litter decay rate, he recognised that the correlation was due to the affect the AET had on decomposer organisms. Whitford *et al.* (1981) suggested that these effects were a reflection of the efficiency of the decomposer organisms themselves, and the interactions between different groups of these organisms (those causing chemical breakdown, and those causing physical breakdown of the CWD material). However; higher soil moisture can have an affect on CWD decay, to some extent, if the log has below-optimum moisture levels, especially where the log is directly contacting the moister-soil, as found by (Næsset 1999a).

TEMPERATURE (& ALTITUDE). Decomposition rates of organic material are strongly influenced by temperature (Abbott and Crossley 1982; Spies and Cline 1988; Pyle and Brown 1999; Wang *et al.* 2002). Decomposition rates are proportional to heat availability, that is, decomposition rates are higher in climates with higher temperatures (Erickson *et al.* 1985; Harmon *et al.* 1987, 2000; Torres 1994; Woldendorp *et al.* 2002a; Brown *et al.* 2003). This is due to the affect of the decomposer organisms having a higher metabolic rate at higher temperatures (Fahey 1983).

Daubenmire and Prusso (1963) and Harmon *et al.* (2000) suggest that there is a threshold for the relationship between heat and decomposition rate. They claim there is an optimum temperature where the decomposer organisms are most efficient, beyond which their efficiency decreases with increasing temperature. This is undoubtedly due to the affect the heat has on the enzymes of the decomposer organisms. Temperature has an affect on CWD decomposition by affecting the efficiency of the enzymes used by the decomposer community, and, indeed, affecting the decomposer-community itself based on which organisms have the most efficient enzymes for the ambient temperature (Sinsabaugh *et al.* 1991). Moorhead *et al.* (1996) states that decomposer micro-organisms generally operate within a temperature range between 0°C and 50°C, with optimal temperatures between 30-40°C. Indeed, Moorhead and Reynolds (1991) found increasing decomposition, due to increasing microbial metabolism, with temperature increase up to 30°-40°, but decreasing decomposition with temperatures above this range. Li *et al.* (1992) found a declining growth in CWD of the resident N_2-fixing *Bacillus* species with temperatures over 35°C.

Boddy and Swift (1984) and Edmonds *et al.* (1986) did not find any differences in decay rate due to seasonal differences in decay commencement. That is, it did not matter whether decay of the CWD started in summer or winter; the decay rate was the same. This is undoubtedly due to the prolonged CWD decay, causing a dampening effect for single years, or season, of decay commencement. Boddy and Swift (1984) did note, however, that the instantaneous decay rate was lower in winter, due to the lower temperatures.

Savely (1939) found that logs in shade moderated temperatures, with minimum and maximum temperatures measured in logs less-extreme than that of the surrounding air (although mean temperatures were similar to air temperature), with a corresponding amelioration against rapid temperature changes. Savely (1939) also found, however, that logs exposed to direct sunlight can have greater temperature maximums under the bark than the surrounding air temperature. The upper-surface of logs in full-sun will become markedly hotter than the lower surface, which is in the shade of the upper-log, creating a large temperature-gradient within the log (Graham 1925). In full-sun the temperature of a log's upper-surface is influenced more by insolation than ambient air temperature (Graham 1925). Consequently, microclimate affects CWD decomposition (Boddy 1983a), and forest canopy-cover affects microclimate (Uhl and Kauffman 1990), therefore forest canopy-cover has an affect on the decay rates of CWD. The further from the surface a resident-organism occurs, the lesser the temperature fluctuations it experiences (Graham 1925). Smaller-diameter logs have greater temperature fluctuations than larger-diameter logs (Graham 1925).

MOISTURE AND TEMPERATURE INTERACTIONS. Generally, CWD decomposition is driven by the physiology of the decomposer micro-organisms (Moorhead *et al.* 1996; Delaney *et al.* 1998; Hicks *et al.* 2003). Boddy (1983b), in a laboratory study, found that as temperature alone increased, decomposition decreased, and as humidity alone increased, decomposition decreased, but as temperature and humidity increased together, decomposition increased. This shows a synergistic-effect between temperature and moisture availability. Hicks *et al.* (2003) found that N_2-fixation by bacteria within CWD was significantly higher in sites that were both wetter and warmer; higher N_2-fixation rates have been associated with faster decay rates (see 2.1.4.1 for a discussion of this point). The reason behind this interaction-effect may be that as temperature increases, enzymatic efficiency in the decomposer organisms increases, but the higher temperature also increases evaporation rate, which is detrimental to the

decomposer organisms, consequently, an increase in temperature alone may actually cause a decrease in available moisture resulting in a decrease in metabolism.

Erickson *et al.* (1985) found that the decomposition rate of *Pinus ponderosa* decreased with a decrease in available moisture, they also found that the decomposition rate of *Abies amabilis* Dougl. ex Forbes decreased with decreasing temperature; a finding showing a positive relationship between decomposition rate and the availability of moisture and heat (temperature). However, Edmonds *et al.* (1986) found that the decomposition rate of *P. menziesii* was not correlated to moisture content. This shows that there is a confounding of factors in the control of decomposition rates, and species-specific physico-chemical factors may play a major role in determining which environmental factors will control the efficiency of the decay process.

Temperature and moisture interact; moisture moderates temperature fluctuations, and temperature influences the evaporation-rate of moisture (Boddy 1983a). Temperature often determines the moisture content of CWD, as warmer air can hold more moisture than cooler air. This leads to a greater evaporation of water from the CWD surfaces, resulting in lower levels of available moisture in the CWD. Higher humidity reduces the evaporation rate. Consequently, there is a synergistic effect between temperature and humidity, with increases in both providing conditions closest to optimal for the decomposer organisms, with a concomitant increase in metabolism and CO_2-release until anaerobic conditions are reached and metabolism decreases (Boddy 1983b). As far as CWD decomposition is concerned, temperature and moisture-availability are inextricably associated (Boddy 1983b; Delaney *et al.* 1998), and, as such, it is usually difficult to determine the exact contribution each makes to the decay rate (Edmonds *et al.* 1986).

Large inter-annual variations in climate, especially temperature and rainfall, create parallel changes in CWD substrate microclimate, and result in heterogeneity of decay rate (Woods and Raison 1982; Boddy 1983a).

CHEMICAL PROPERTIES

INTRODUCTION. The chemical composition of plant debris has generally been considered a major factor controlling decay rates (Christensen 1977; Fogel and Cromack 1977; Melillo *et al.* 1982; Brown *et al.* 1996; Chambers *et al.* 2000). Nutrients, toxins, and resilient compounds such as lignin, play an important role in the determination of the rate of decay (Scheffer 1957; Scheffer and Cowling 1966; Wieder

and Lang 1982; Moorhead and Reynolds 1991; Rowland and Roberts 1999; Chambers *et al.* 2000 Ganjegunte *et al.* 2004). The cell-wall structure of wood is primarily composed of cellulose, hemicellulose, and lignin (Boddy 1983a). Differences in decay rates have been observed between species (Arthur *et al.* 1993), and differences in chemical makeup would be a major contributor to these differences (Scheffer and Cowling 1966). The presence of species-specific toxic compounds inhibits microbial colonisation of wood, resulting in a reduced decay rate (Daubenmire and Prusso 1963). The rate-of-decay of a CWD-piece may serve as an indicator of substrate quality (Moorhead and Reynolds 1991).

ENZYME ACTIVITY. There are three classes of wood substrate components, (i) polar and non-polar extractives (soluble component) which have a high nutrient content and decay rapidly, (ii) acid insoluble fractions (lignins) which decompose slowly, and (iii) acid soluble fractions (cellulose and hemicellulose) which decay rapidly if accompanied by sufficient nutrients for decomposer metabolism, but otherwise are decomposed slowly (Moorhead *et al.* 1996). The celluloses are, however, easier to digest than lignin (MacMillan 1981; Wieder and Lang 1982). The three classes of wood substrate components (extractives, acid insoluble fraction, and acid soluble fraction) are degraded by glucosidases, oxidases, and cellulases, respectively (Moorhead and Sinsabaugh 2000).

Patterns of plant litter decay are positively correlated with enzymatic activity (Sinsabaugh *et al.* 1991). Sinsabaugh *et al.* (1992) found a successional sequence of enzymes as decomposing wood progressed through the decay process. In a model simulation of enzymatic affects on decomposition, Moorhead and Sinsabaugh (2000) found that the simpler molecules were degraded by the initial colonisers of the wood, as these are more "energetically efficient" than the breakdown of more complex molecules. The energy-rich, and labile, carbohydrates are relatively quickly metabolised, and depleted, by decomposer organisms (Ganjegunte *et al.* 2001; Bütler *et al.* 2007), which correlates with the initial rapid rate-of-decay followed by an ever-slowing decay rate. There are two classes of carbohydrates: (i) non-structural carbohydrates are found in the cytoplasm and are readily available to micro-organisms attacking the CWD, whereas (ii) structural carbohydrates are part of the cell walls, and are degraded at a much slower rate than the non-structural carbohydrates (Tainter and McMinn 1999). The different enzymes required to break down the different compounds, which change proportions as the decay process proceeds, would account

for the successional pattern of enzymes found in decomposing wood by Sinsabaugh *et al.* (1992). Additionally, many enzymes would only appear in the CWD after suitable substrates became available from the creation of these substrates by previous enzyme activity. Sinsabaugh *et al.* (1992) found enzyme activity levels were more strongly correlated to CWD decay stage than site factors or age. This shows a greater influence by substrate chemistry than microclimate on the decomposers.

LIGNIN CONCENTRATIONS. Woody material is higher in initial lignin concentration than non-woody material (Maser *et al.* 1988; Chambers *et al.* 2000). Edmonds *et al.* (1986) found, in a study of a conifer (*P. menziesii*) and an angiosperm (*A. rubra*), that smaller diameter wood had higher lignin concentrations, resulting in an increased lignin:N ratio. As decomposition proceeds, the decay-resistant lignin increases in concentration (Bütler *et al.* 2007). As lignin content increases proportionally, the decomposition rate of CWD decreases (Fogel and Cromack 1977; Meentemeyer 1978; Melillo *et al.* 1982; Wieder and Lang 1982; Moorhead *et al.* 1996; Rowland and Roberts 1999). Fogel and Cromack (1977) found that initial lignin concentration had a strong influence on litter decay rate. However, in a study of angiosperm leaf litter in the United States (New Hampshire), Melillo *et al.* (1982) found a poor correlation between the decomposition constant (*k*) and initial lignin content. They did find, however, a strong negative linear correlation between *k* and initial-lignin:initial-nitrogen ratio ($r^2 = 0.89$). (However, this is likely to be more of a positive correlation between the initial N content and *k*.) The study of Fogel and Cromack (1977), however, indicate that lignin concentration has a greater influence on the decomposition rate than does the nitrogen concentration. The guaiacyl-based lignin of conifers is more decay-resistant than the syringyl-containing (guaiacyl- and syringyl-based) lignin of angiosperms (Boerjan *et al.* 2003; Ganjegunte *et al.* 2004). However, Erickson *et al.* (1985) found no correlation between initial lignin content and decomposition rate of four species of conifer; although their study was conducted after clearfelling, which created a harsh environment where moisture and temperature extremes were greater than what would have been experienced under a natural forest canopy.

BARK VS. WOOD. The decay rates of the bark and wood fractions of CWD differ markedly (Idol *et al.* 2001). Generally, bark decomposes faster than the wood fraction (Schowalter *et al.* 1998), but occasionally bark is found to be more decay resistant than sapwood (e.g. Fogel and Cromack 1977; Abbott and Crossley 1982; Ganjegunte *et al.* 2004). A higher decay resistance in the bark may explain why some CWD has a

distinct lag, before the initial rapid sapwood decomposition commences, in the early stages of decay. (It may take some time before the bark has been decomposed before the more labile sapwood component is accessible to the decomposers.)

NITROGEN. Nitrogen content has been found to be a major factor in controlling the decay rate of CWD in some studies (e.g. Findlay 1934; Merrill and Cowling 1965; Cowling and Merrill 1966; Foster and Lang 1982), although Merrill and Cowling (1966a) found that at least some species of fungi can adapt their internal N-content to adjust for lowered N-concentrations in wood. In CWD, nitrogen is probably the nutrient most limiting to decomposition (Cowling and Merrill 1966). Nutrient concentrations, such as N, have an affect on decay rates due to their requirement for the growth of the decomposer organisms (Merrill and Cowling 1966b). Currie and Nadelhoffer (2002) found that N concentration varied widely between CWD pieces of the same age; this was associated with widely varying wood-densities, which is suggestive of inconsistent decay. A thorough discussion on nitrogen dynamics in CWD, including N_2-fixation, is given in 2.1.4.1.

C:N RATIO. CWD and other woody-litter has a higher C:N ratio than non-woody litter (Currie and Nadelhoffer 2002). Wieder and Lang (1982) propose that higher C/N ratios result in increased decay resistance. This, however, is likely due to the low N concentrations, as C remains relatively stable at about 50% (Foster and Lang 1982; Mattson *et al.* 1987; Schowalter 1992; Karjalainen 1996; Schowalter *et al.* 1998; Laiho and Prescott 1999; Mackensen and Bauhus 1999; Chambers *et al.* 2000; Robertson *et al.* 2000; Woldendorp 2000; Chojnacky and Heath 2002; Currie and Nadelhoffer 2002; Mackensen *et al.* 2003; Ganjegunte *et al.* 2004; Bütler *et al.* 2007), which suggests low nutrient availability, resulting in slower decomposer growth, and, consequently, slower decomposition of the wood.

WOOD DENSITY. Wood density varies between species, and as a result has an affect on decay rates (Woldendorp *et al.* 2002a). Species with lower wood density decay faster than species with higher wood density (Mackensen and Bauhus 1999). Barber and Van Lear (1984) found that the variability of CWD density increased with age, due to microsite variations in moisture and temperature and random variation in decomposer colonisation of the wood, leading to an increasingly heterogeneous pattern in CWD decay. Barber and Van Lear (1984) and Clark *et al.* (2002) also found that the decomposition process became more variable as the log progressed through the decomposition process.

Graham and Cromack (1982) found that wood-density variability increased with increasing log-diameter; this pattern may be partly due to advanced decay in the earlier-colonised outer-wood but only initial decay in the later-colonised inner-wood. This decay-variability with diameter can make decay-state classification problematic, as a system that works for smaller-diameter logs may not work with larger-diameter logs, and *vice versa* (Sollins 1982).

Although it is generally accepted that nutrient availability and toxins have an affect on CWD decay rates, it is interesting that Melin (1930) and Daubenmire and Prusso (1963) found no correlation between chemical contents of leaf litter and decay rates. This suggests that other factors may, at least occasionally, be more important in determining the decay rate of plant litter (Melin 1930), including both CWD and fine litter.

ASPECT

It is reasonable to assume that aspect would have some affect on the decomposition of CWD (Næsset 1999a). Although many authors report aspect of study sites, they do not report the significance, or otherwise, of aspect on decomposition rates. Næsset (1999b) found aspect a significant factor in the decay of *Picea abies* (L.) Karst. CWD. Edmonds *et al.* (1986), however, reported that aspect (north versus south) did not have a significant affect on the decomposition rates of *P. menziesii* and *A. rubra*, based on mass loss.

This lack of reporting the affect of aspect is probably due to the nature of reporting aspect as compass points (e.g. NE, SSW, etc.; geographic coordinates). Clearly, a method of enumeration of aspect is required, so that it can be incorporated into parametric analyses of factors affecting decomposition rates. A proposed method of enumerating aspect can be found in Appendix A.

One reason for the possible non-reporting of aspects is non-significance found due to the confounding affect of temperature and moisture, where aspects facing the equator have higher heat-availability, but lower moisture-availability due to greater evaporation, and *vice versa* for poleward-facing aspects (Brown *et al.* 1998).

SUPPORTING MATRIX QUALITY

CWD lying prostrate on the ground have higher decay rates than elevated CWD (McFee and Stone 1966; Fahey 1983; Barber and Van Lear 1984; Erickson *et al.* 1985;

Mattson *et al.* 1987; Mackensen and Bauhus 1999); Næsset 1999b; Wang *et al.* 2002. Barber and Van Lear (1984) found that logging slash of the conifer *Pinus taeda* L. placed on the soil surface decayed 50% faster than elevated slash. Erickson *et al.* (1985) found that *P. menziesii* wood lying prostrate on the soil surface decayed at a significantly faster rate than elevated wood. Edmonds *et al.* (1986) also found that *P. menziesii* wood lying prostrate decayed faster than elevated wood, but the difference was not significant. The higher decay rates for prostrate wood, is due to higher moisture conditions occurring when the CWD is in contact with the ground, which affords a more favourable environment for the decomposer organisms (Fahey 1983; Barber and Van Lear 1984). Ground contact provides direct access for fungal hyphae residing in the soil, leading to faster colonisation of the CWD (Barber and Van Lear 1984). Decay rates for logs placed flat on the ground represent the maximum decay rate for a given site (Alban and Pastor 1993). Edmonds *et al.* (1986) found that buried *P. menziesii* wood decayed significantly faster than wood lying prostrate on the soil surface. They effect of burying the wood was less pronounced for the angiosperm *A. rubra*.

Barber and Van Lear (1984) found that logging slash in contact with the ground experienced greater rates of leaching than elevated slash, which they assumed to be due to the prostrate CWD remaining wetter for longer after rain. The prostrate CWD, however, would also have a greater effective rain interception surface area (per volume) than any slash that was not lying horizontal, and the greater amount of rain interception should account for at least some of the variation in leaching rates between prostrate and elevated CWD.

WOOD SUBSTRATE SURFACE AREA : VOLUME RATIO

Log diameter, which affects the surface-area:volume ratio of the log, and log shape, has an affect on the rate of decay (Spies and Cline 1988; Pyle and Brown 1999; Næsset 1999a; Currie and Nadelhoffer 2002).

SMALLER DECAYS FASTER. There is a common assumption that smaller diameter CWD decays faster than larger diameter CWD, due to the greater surface area to volume ratio (Maser *et al.* 1988; Spies and Cline 1988; Busse 1994; MacMillan 1981). Abbott and Crossley (1982) found that smaller diameter branches, of the temperate angiosperm *Q. prinus*, decomposed faster than larger diameter ones. Edmonds *et al.* (1986), studying a temperate angiosperm (*A. rubra*) and softwood (*P. menziesii*), also found that smaller

diameter logs decomposed faster than larger diameter logs. Conifer CWD studies by Graham and Cromack (1982), Sollins (1982), and Harmon *et al.* (1987) all found smaller diameter CWD decaying faster than larger diameter CWD. MacMillan (1981) attributes this higher decay rate of smaller diameter CWD to the higher surface area to volume ratio, as a greater number of decomposer organisms can infect the CWD piece for its given volume.

SMALLER DECAYS SLOWER. However, Barber and Van Lear (1984) found that smaller diameter CWD of the temperate conifer *P. taeda* decayed slower than CWD with larger diameters. Erickson *et al.* (1985) also found this trend with two other species of temperate conifer (*P. menziesii* and *Tsuga heterophylla* (Raf.) Sarg.). Næsset (1999b) also found smaller-diameter CWD of the conifer *P. abies* decaying slower than the larger-diameter samples; although this may have been due to treatment-effects as the smaller-diameter CWD was elevated, whilst the larger-diameter CWD was prostrate due to post-felling limbing.

CASE HARDENING. Erickson *et al.* (1985) found that the dry summers of Washington (NW USA) dehydrated smaller diameter CWD, of four species of conifer, to such an extent that decomposition was lower than that of larger diameter CWD. The dehydration effects of the summers were so pronounced, that annual decay rates of the smaller diameter CWD were lower than that of the larger diameter material, showing that the dehydration of the smaller CWD had an overriding effect for the relatively benign conditions of the other seasons in the year.

There is enormous variance in the decay rates of smaller-diameter pieces of CWD, which can decompose either faster or slower than larger pieces of CWD. Moisture levels are more variable in smaller-diameter woody debris, as they have a greater surface-area:volume ratio (Griffith and Boddy 1991a). This variability is a function of the available-moisture régime at the site (Harmon *et al.* 1986). Barber and Van Lear (1984) and Erickson *et al.* (1985) attribute the lower decay rates of the smaller diameter CWD to desiccation. Larger CWD is less prone to complete desiccation, due to the lower surface area to volume ratio, and the greater insulation provided by the thickness of the wood (Barber and Van Lear 1984). Erickson *et al.* (1985) suggest that in drier climates the greater surface area to volume ratio of smaller diameter CWD functions more as a moisture-loss medium, than a medium for greater colonisation densities of decomposer organisms, which would result in lower decay rates. Savely (1939) found that smaller-diameter logs retain less moisture in dry conditions than those with larger

diameters. Once desiccated, smaller diameter CWD can become temporarily hydrophobic, initially resisting re-hydration when moisture levels increase in the environment (Erickson *et al.* 1985). This effect was termed the "hysteresis effect" by Erickson *et al.* (1985).

It is anticipated that desiccation of CWD may be increased by galleries made by tunnelling invertebrates and cracks in the wood allowing dry air into the inner wood. This would allow the moisture that would normally be insulated toward the centre of the larger diameter CWD to evaporate to the atmosphere.

The pattern of desiccation of CWD in dry, or seasonally dry, climates has been termed 'case hardening' by Barber and Van Lear (1984), Erickson *et al.* (1985), Edmonds *et al.* (1986), Alban and Pastor (1993), and USDA Forest Service (2001). This term is actually a misnomer. 'Case hardening' is a term taken from metallurgy, and refers to the process of hardening the exterior surface of a metal object as a means of increasing its durability and service life. It would be better to think of the process, as far as wood decomposition is concerned, simply as 'wood desiccation'.

2.1.1.4 *Effect of CWD Length*

Length of CWD also has an affect on decomposition, with shorter lengths having faster decomposition rates (Harmon *et al.* 2000). This is due to the lower volume of wood for a given diameter, affording greater infection efficiency by the decomposer organisms. Consequently, the length of logging slash left on-site will be a major factor in determining the decay rate of the slash. The affect of CWD length between studies of whole tree-fall and logging slash makes meaningful comparisons between these studies difficult. The length-effect is only pertinent to shorter CWD pieces, as the extra surface area of the ends accounts for an ever decreasing proportion of the total surface area as CWD piece length increases.

2.1.1.5 *Causes of Decay Resistance*

When living plants are attacked by fungi, ethylene production is stimulated (Salisbury and Ross 1992), which in turn stimulates the production of the enzymes chitinase and β-1, 3-glucanase that degrade the cell walls of the intruding hyphae (Abeles *et al.* 1971); this is part of the plant's defence-system (Boller 1988). It is thought that ethylene release, which occurs when a seed plant is injured, initiates mechanisms against fungal infection (Salisbury and Ross 1992). However, once plants

have died, they cannot produce ethylene to ward off fungal degradation of structural compounds.

Decay resistance in dead wood is caused by the residual tannins and fungitoxic extractives formed during the transformation of sapwood to heartwood, and it is usual for several fungitoxins to be present in the wood (Rudman 1961; Da Costa 1975; MacMillan 1981). The different fungitoxins present in any specific piece of wood, and the different concentrations, is the major determining factor of decay resistance in wood (Da Costa 1975; Blanchette 1995; Blanchette *et al.* 2004). Higher concentrations of these extractives in the heartwood make it more resistant to decay than the sapwood (Rudman 1961; MacMillan 1981). The influence of extractives in determining the decay resistance of wood is complex (Scheffer and Cowling 1966; Harmon *et al.* 1986), as only some of the extractives enhance decay resistance, and the concentrations can change (Rudman 1961; Brown *et al.* 1996). This is especially true of decomposing wood, as the water-soluble extractives are leached by water movement through the wood (Baker *et al.* 1983). Many of the extractives also convey a measure of resistance to attack by wood-destroying invertebrates (Bultman and Southwell 1976).

Many polyphenolic substances are toxic to fungi, and can contribute to decay resistance in wood (Scheffer 1957; Bultman and Southwell 1976; Chambers *et al.* 2000). Decay resistance in eucalypts appears to be principally due the presence of polyphenolic substances, especially ellagitannins (Da Costa 1975). Not all eucalypts, however, have high decay resistance; *Eucalyptus regnans* F.Muell. decomposes readily compared to most eucalypts (Da Costa 1975).

Tannins are a sub-group of the polyphenols, and, as such, are regarded as secondary compounds (Benoit *et al.* 1968; Cameron and LaPoint 1978; Kraus *et al.* 2003). Tannins have several functions in the living tree, and one of the most important is in deterring herbivory and attack by bacterial and fungal pathogens (Benoit *et al.* 1968; Cameron and LaPoint 1978; Kraus *et al.* 2003), which has the effect of inhibiting decomposition (Benoit *et al.* 1968; Kraus *et al.* 2003); at least until the tannins have been leached (Cameron and LaPoint 1978). Tannins have been found to be non-toxic (Benoit *et al.* 1968; Cameron and LaPoint 1978), but inhibit growth of decomposer organisms by inhibiting some of their enzymes (Goldstein and Swain 1965; Kraus *et al.* 2003), which impacts upon the metabolism of the decomposer organisms (Cameron and LaPoint 1978). Preston *et al.* (1997) showed that what has often been interpreted as lignin in wood (Klason lignin), actually includes tannin and cutin as well as lignin.

Consequently, the often-espoused relationship between decay-resistance and lignin may show, at least in part, a relationship between decay-resistance and tannin-concentration (Kraus *et al.* 2003).

Scheffer (1957) found the outer heartwood of the conifer *Thuja plicata* Donn ex D. Don to be more decay-resistant than the inner heartwood; with a progressive decrease in decay-resistance from the outer heartwood to the inner heartwood; Scheffer (1957) suggest that this may be the normal pattern of heartwood decay-resistance. However, this decrease in decay-resistance from the outer heartwood to the inner heartwood may be the result of increasing N-content from the outer heartwood to the inner heartwood (see 2.1.4.1 for a discussion of this point). Consequently, the pattern may be more of a factor of increasing 'decay-conductance' from the outer heartwood to the inner heartwood (due to increasing N-concentration) than a factor of decreasing decay-resistance.

2.1.1.6 Discussion

Edmonds *et al.* (1986) found that smaller diameter wood had higher lignin content than larger diameter wood. Fogel and Cromack (1977) showed that initial lignin concentration has a strong influence on wood decomposition, with higher lignin concentrations resulting in lower decomposition rates. This results in somewhat of an antinomy, where the larger diameter wood has a lower lignin concentration, enhancing decomposition, but has a lower surface-to-volume ratio, reducing decomposition. Due to the greater proportion of decay-resistant materials in wood, compared to the other components of forest litter, and the resulting slow decomposition rate, dead woody material accumulates in higher proportions in the soil than the other components (Christensen 1977). This makes CWD far more effective at long-term storage of C than the other forms of litter.

Not all investigators, however, have found that diameter affects decomposition rates. Foster and Lang (1982) found no affect of bole diameter on the decomposition rate of the temperate angiosperm *Picea rubens* Sarg.. In a study of temperate angiosperms (*P. tremuloides* and *Picea glauca* (Moench) Voss) and conifers (*Pinus banksiana* Lamb. and *Pinus resinosa* Ait.), Alban and Pastor (1993) also failed to find a relationship between diameter and decay rate (sample diameter sizes ranged from 5-24 cm).

Despite the lack of correlation between CWD diameter and decomposition rate in the studies of Foster and Lang (1982) and Alban and Pastor (1993), CWD diameter

generally appears to influence the decomposition rate of CWD. As a generalisation, smaller diameter CWD have a greater sapwood-to-heartwood ratio, which can be expected to have an increased decay rate, due to the higher decay rate of the sapwood (MacMillan 1981).

The study of the decay rate over the natural climatic variation, for a species, is necessary for the development of models predicting decay rates for the species over a wide range of site conditions (Alban and Pastor 1993). Meentemeyer (1978) found moisture availability had a greater influence on decomposition rates than lignin content. This shows the reality of the situation, where lignin is one of the chemical factors determining the maximum potential decomposition rate, but climatic conditions determine the actual decomposition rate that occurs within the maximum potential decomposition rate. Erickson *et al.* (1985) suggest that the decay of logs at a community or regional scale is more strongly correlated with physical factors and climate than with species-specific chemical compounds; this undoubtedly would be due to the great variability in chemistry between species.

Gosz *et al.* (1973) found that angiosperm branches, of 5 mm diameter, decomposed faster than conifer branches of the same diameter. This is supported by Edmonds *et al.* (1986) who found that the wood of the angiosperm *A. rubra* (k = 0.035-0.517 yr^{-1}) decayed faster than that of the conifer *P. menziesii* (k = 0.006-0.205 yr^{-1}). (Note, k is the decay-model constant, for the single-exponential model, and represents the proportional rate-of-decay for a time-period. See section 2.2.5.3 *Single-Exponential Model* for a description of the model and its usage.) Edmonds *et al.* (1986) found that buried wood decomposed faster than wood lying on the ground, which in turn decomposed faster than elevated wood.

A test of differences in rates-of-decomposition between angiosperm and conifer CWD was done; using the decomposition-model constant (k-values) of the single-exponential model. Collection of metadata from the literature resulted in 211 k-values being used; 121 angiosperms and 90 conifers. The comparison was done with a t-test, and required a natural-logarithm transformation (see Figure 2-1 a) and b) for the transformation affect) to achieve homoscedasticity (equality of variances; F-test statistic) before the t-test could be done. The t-test showed a significant difference between the single-exponential model constants (k-values) for angiosperms *vs.* conifer CWD ($p < 0.0001$); that is, angiosperm CWD decays significantly faster than conifer CWD. Arthur *et al.* (1993) found that decay of boles of angiosperm species (in a

northern hemisphere angiosperm-dominated forest) was rapid in comparison with conifer forests, and the result of this meta-analyses agrees with their findings.

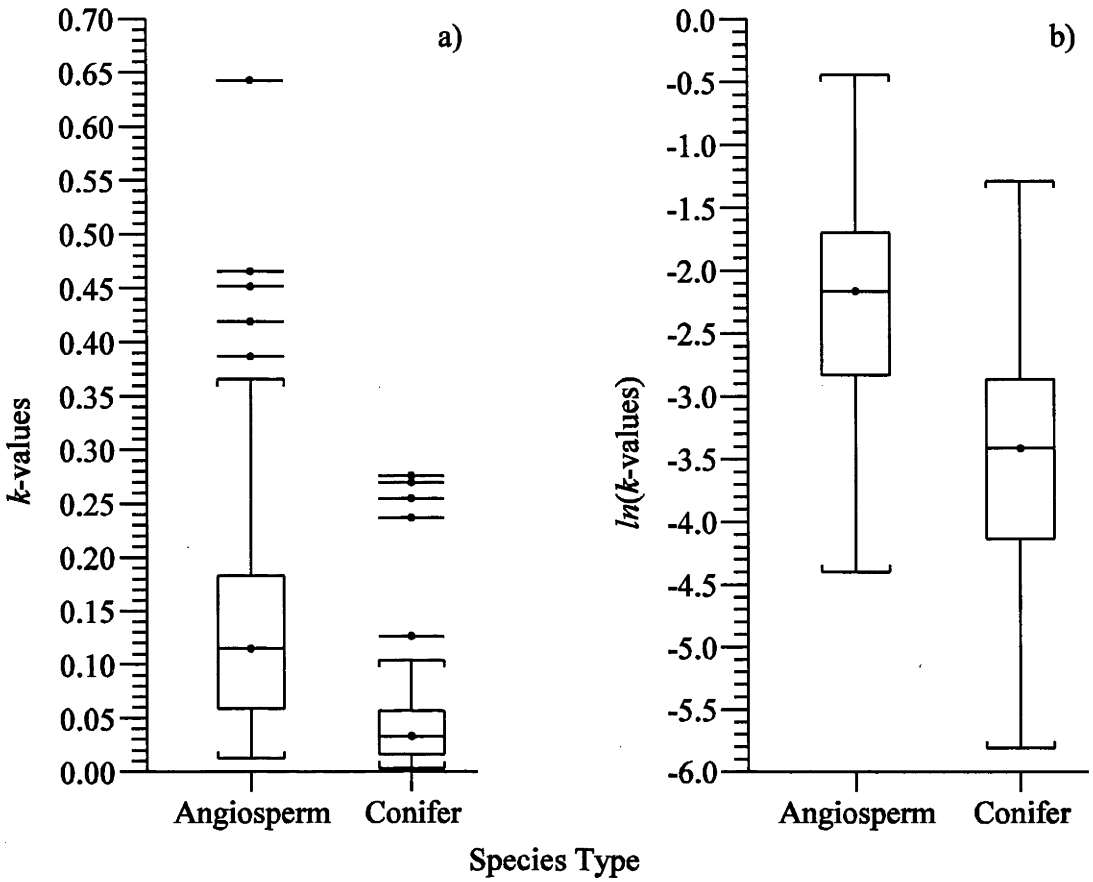


Figure 2-1. Comparison of angiosperm and conifer CWD *k*-values from the single-exponential model — *ln*-transformation was necessary to achieve homoscedasticity. Data is for prostrate CWD, with the *t*-test showing $p < 0.0001$.

Brown *et al.* (1996) conclude that in wetter climates, where available moisture is not limiting, the smaller diameter CWD decays faster due to the higher concentrations of nutrients affording a more favourable substrate than the larger CWD. Whereas, in dry climates, moisture becomes limiting, and becomes dominant over nutrient availability in controlling decay rates. In moist environments, the large surface area to volume ratio of the smaller CWD favours greater colonisation by decomposer organisms (Barber and Van Lear 1984), but in dry environments, the greater ratio retards decomposition due to the faster loss of moisture. It is possible for smaller diameter CWD, in dry environments, to have an initial rapid decomposition rate (due to rapid decomposer colonisation), but experience a relative (compared to larger CWD) rapid decrease in decomposition rate as it desiccates.

Erickson *et al.* (1985) found that undecomposed smaller diameter residue wood had a greater density than the larger diameter wood in a study of four species of conifer. This increased density, in the smaller diameter wood, may restrict the entry of liquid water

into dry wood, but provide minimal resistance to the release of water vapour during the drying process. Consequently, smaller diameter conifer wood would dry out faster, and re-hydrate slower, than larger diameter wood. Moisture levels are more variable in smaller-diameter woody debris, as they have a greater surface-area:volume ratio (Griffith and Boddy 1991a). Savely (1939) found that smaller-diameter logs retain less moisture in dry conditions than those with larger diameters. In climates that are seasonally dry, smaller-diameter CWD will show a greater variability in the instantaneous decay rate.

The pattern here is that, in moister climates where desiccation of CWD rarely occurs, the smaller pieces of CWD will decay faster than larger pieces of CWD. However, in drier climates, or seasonally dry climates, where the smaller pieces are prone to desiccation, the smaller CWD will decay at a slower rate than the larger pieces (Barber and Van Lear 1984; Edmonds *et al.* 1986). The problem, for investigators, is that all CWD decay rates vary with changes in environmental moisture régimes, but the variability is most pronounced in the decay rates of smaller CWD.

It seems that in moist environments smaller diameter CWD has a higher decomposition rate than larger diameter CWD. However, in dry climates, or drier seasons, the smaller diameter CWD has a lower decomposition rate due to the total drying out of the substrate, providing a hostile environment for decomposer organisms. The larger diameter CWD retains moisture nearer the centre of the substrate for a longer time, providing a more benign environment for the decomposer community. The retention of a viable decomposer community within the centre of larger diameter CWD, also affords a quicker colonisation of the outer wood when favourable moisture conditions return.

Decay rates can also be influenced by the size of vessels and tracheids in the wood, as smaller-diameter conduits retain water longer in dry conditions than do species with larger-diameter structures (Griffith and Boddy 1991a). Saturated wood allows some measure of anoxia (Boddy 1983a) due to reduced diffusion of gases in the vessels and tracheids (Boddy 1983b). The length of the CWD-piece also affects gas-diffusion as longer-logs have a higher resistance for gas-exchange with the atmosphere (Boddy 1983b). This effect will be more to do with differences between divisions, as there is considerable variation and overlap between vessel and tracheid diameters, despite the vessels of angiosperms having larger maximum diameters than the maximum-diameters achieved by the tracheids of conifers (Sperry *et al.* 2006). It is reasonable to assume

that angiosperms, with their overall greater vessel-diameters 'on average', would, in the early stages of decay, experience greater variability in moisture content and may also be prone to slightly higher leaching-rates. The larger vessels would facilitate easier infection by decomposer organisms (Ferguson 2005), affording a potentially faster decomposition rate than that of the conifers with their tracheids.

Eaton and Lawrence (2006) stated that fire might facilitate an increased decay rate by affording greater decomposer access to the wood by removing bark. It is hard to see how the earlier removal of bark would increase the overall decomposition rate, as earlier bark-removal would just create a phase-shift by allowing earlier colonisation by the decomposer organisms. This phase-shift would allow the decomposition process to finish sooner, but it would be achieved without an increase in the rate of decay. Heat from fire, however, may also denature many toxins in CWD-wood, and reduce colonisation time by decomposer organisms that would normally have to wait until the toxins were leached from the wood. However, exposure to fire can potentially slow decomposition by reducing the nutrient content of CWD; Stewart and Flinn (1985) found that fire reduced the nutrient concentration of eucalypt CWD.

Due to differences between species, at the species level climate does not have as strong an influence as substrate quality in determining decay rates compared to the community or regional level (Fogel and Cromack 1977; Abbott and Crossley 1982; Erickson *et al.* 1985). Scheffer (1957) found decay-resistance can vary within a single tree, postulating that it can somewhat be attributed to non-uniform distribution of decay-inhibiting compounds. However, at the continental scale, climate is a more important regulator of decay rates than substrate quality (Meentemeyer 1978). The reduced importance of substrate quality over larger areas is due to the greater mix of species, and the lessening of dominance of any particular species, creating a dampening affect on species differences. Besides substrate quality, anthropogenic influences also complicate the assessment of climate affects on CWD decomposition (Moorhead *et al.* 1996).

Generally, moisture and temperature régime has the greatest influence on CWD decomposition rates (Edmonds *et al.* 1986; Moorhead *et al.* 1996). Physical factors influence CWD decomposition solely on their affect on the temperature and moisture régime of individual CWD pieces. However, in some species substrate chemistry can play a major part in determining CWD decomposition rates, such as the significant affect of soda solubility found for the angiosperm *A. rubra* (red alder) by Edmonds *et*

al. (1986). However, the relative affect of plant-manufactured nutrients and toxins decreases with length of time the CWD-piece has existed, as they are leached as well as being consumed and modified by decomposer organisms; making the resilient structural-compounds, like lignin, and microclimate more determining of the maximum potential rate-of-decay. There is a great need to clarify the relative importance of external (micro-environmental) and internal (chemical) factors determining rates of decomposition (Preston *et al.* 2006).

2.1.2 FACTORS DRIVING CWD DECAY

The decomposition of CWD is primarily due to the actions of decomposer organisms, with potentially some molecular denaturing occurring during exposure to extremely hot weather on exposed wood after tree-fall (or clearing). Some loss of soluble material undoubtedly occurs due to water movement through the CWD matrix (Swift 1977). Much of the C in the CWD matrix is lost to the atmosphere through decomposer organism respiration, with the C being cleaved during digestion, then oxidised and released to the surrounding environment as CO_2. Some of the ingested C is incorporated into the decomposer organism and released to the surrounding environment upon death of the organism; some as frass eventually incorporated into the soil, some digested by other micro-organisms leading to CO_2 release to the environment.

The decomposition of CWD, and the associated nutrient cycling and biological cycling of successional organisms, is vital for the maintenance of forest health, and, therefore, is important for ecosystem functioning (Blanchette 1995).

2.1.2.1 Microbial Breakdown of CWD

Microbial-breakdown occurs from the action of micro-organisms and fungi (Scheffer and Cowling 1966; Mattson *et al.* 1987); yeasts, which are single-cell fungi in the Division Mycophycota (Knox *et al.* 1995), often are referred to as micro-organisms. "Decomposer organisms" is the term used to describe the micro-organisms and fungi that are responsible for the microbial breakdown of CWD. As stated above, decomposer organisms include micro-organisms and fungi, however, occasionally the term usage also includes plants (invading-roots; e.g. Maser *et al.* 1988) and invertebrate-animals such as termites (e.g. Harmon *et al.* 1987; Moorhead and Reynolds 1991; Torres 1994; Eggleton *et al.* 1997).

FUNGAL BREAKDOWN

Colonising-fungi are quick to colonise CWD, and are often present in the bark of the living tree (Griffith and Boddy 1990). Secondary molecules produced by fungal decomposition of CWD are vital components of nutrient and energy cycles of forest ecosystems (Temnuhin 1996). The breakdown of wood by fungi provides energy and C for further fungal growth (Madigan *et al.* 1997). Byproducts of fungal decomposition of CWD include CO_2, water, and secondary compounds, all derived from degradation of the wood matrix (Temnuhin 1996).

The water formed during CWD breakdown is effectively metabolic water formed *in situ* by the fungal exudates; some of which is absorbed into the fungal hyphae, the remainder is contained within the wood and available to other decomposer organisms. Consequently, water is continually produced within the CWD by the decomposition process. Even during periods of drought, CWD can accumulate water (Temnuhin 1996), providing the weather is not too hot, and there are no cracks or hollows in the logs which may allow for high levels of water loss to the dry atmosphere.

A small amount of heat is also produced, during fungal decay of CWD, as a byproduct of the degradation of the primary compounds forming the wood matrix (Temnuhin 1996). In cold environments, this may lead to a localised increase in decomposition, due to the enhanced metabolism of the decomposer organisms.

There are three categories of decomposer fungi found in CWD, known as white-rot fungi, brown-rot fungi, and soft-rot fungi (Blanchette 1991, 1995). Hulme and Shields (1970) suggest that initial fungal infection and spread through wood is rapid, afforded by the use of non-structural carbohydrates, which are higher in concentration in the bark than the sapwood or heartwood.

WHITE-ROT. White-rot fungi are members of the division Basidiomycota (Blanchette 1991, 1995). All white-rot fungi are able to degrade lignin, with most also able to degrade the cellulose and hemicellulose of CWD cell walls (Bultman and Southwell 1976; Jurgensen *et al.* 1987; Blanchete 1995; Jurgensen *et al.* 1997; Gutiérrez *et al.* 2002). White-rot fungi generally remove cellulose and lignin in the same proportion, resulting in a constant cellulose:lignin ratio in white-rot decayed wood (Jurgensen *et al.* 1987; Harvey *et al.* 1989). However, some species only degrade lignin, leaving the celluloses intact (Blanchette *et al.* 2004). White-rots are the only fungi capable of decomposing lignin.

BROWN-ROT. Like white-rot fungi, brown-rot fungi are also members of the division Basidiomycota (Blanchette 1991, 1995). Brown-rots attack the cellulose and hemicellulose found in the cell walls of CWD (McFee and Stone 1966; Bultman and Southwell 1976; Jurgensen *et al.* 1987, 1997; Blanchette 1995). Some species of brown-rot fungi can chemically modify lignin, but they do not degrade it; it is left structurally intact (Ashton 1986; Jurgensen *et al.* 1987, 1997; Blanchette 1995). Brown-rot fungi reduce CWD structural integrity by cutting the cellulose microfibrils (Albisetti *et al.* 2003). The same structural weakening in SDTs can also contribute to the increasing likelihood of an SDT falling during windy weather (Albisetti *et al.* 2003). Brown-rot is often associated with termites, and other CWD associated insects (Blanchette 1995).

SOFT-ROT. Initially wood decay fungi were classed as either white-rot or brown rot (Madigan *et al.* 1997), with both groups containing fungi from the divisions Basidiomycota, Ascomycota, and Deuteromycota. A third group is now recognised, known as soft-rots, which are members of the deuteromycetes (fungi imperfecti) and ascomycetes (Bultman and Southwell 1976). The accepted categories now have the white- and brown-rots containing basidiomycetes fungi, and the soft-rots containing fungi from the ascomycetes and deuteromycetes (Blanchette 1991, 1995).

Soft-rot fungi commonly occur in wood where conditions are too extreme for other fungi (Blanchette *et al.* 2004). Because of their greater tolerance for extreme environmental conditions (Blanchette 1991), soft-rots tend to predominate the decomposer organism community in severe environments, especially very wet, very dry, and very cold environments (Blanchette 1995; Blanchette *et al.* 2004). Some soft-rots even tolerate extreme salinity and high UV exposures (Blanchette *et al.* 2004), while others tolerate O_2 concentrations too low for white- and brown rots (Kazemi *et al.* 2001).

DISCUSSION OF THE DIFFERENT DECOMPOSER FUNGI. Brown-rot fungi are the most prevalent fungi found in coniferous forests (McFee and Stone 1966; Jurgensen *et al.* 1989; Blanchette 1995), with white-rot fungi predominating in angiosperm forests (McFee and Stone 1966; Jurgensen *et al.* 1989); this is a generalisation only, as white-rots and brown-rots both occur in conifer and angiosperm CWD. Despite this generalisation, many white-rot fungi are efficient at degrading the lignin of conifer wood (Blanchette 1995); especially the conifer-sapwood (McFee and Stone 1966; Jurgensen *et al.* 1989, 1997). Brown-rotted wood may persist for a long time, as it

contains high concentrations of modified lignin, but extremely low concentrations of carbohydrates (Blanchette 1995). This undoubtedly contributes to the generally slower decay rates of conifers compared to angiosperms (Jurgensen *et al.* 1989).

MacMillan (1981) found a pattern of white-rot fungi infecting the CWD of a mixed *Quercus* L. (angiosperm) forest in the early decay stages, which had been succeeded by brown-rot fungi in the latter decay stages, which is contrary to the generalisation. Supporting the generalisation is the work of Means *et al.* (1985) whom found that the decay of *P. menziesii* (a conifer) followed a pattern whereby white-rot decreased and brown-rot increased as decay progressed. Jurgensen *et al.* (1997), in a study of conifer forests found that the sapwood also had white-rot predominating in early decomposition, but brown-rot predominated later in the decomposition process.

Yee *et al.* (2006), in a study of *E. obliqua* (an angiosperm) forests in southern Tasmania, found that larger-diameter CWD was characterised by heartwood (internal) brown-rot, while smaller-diameter CWD was characterised by white-rot occurring in the outer-log. Interestingly, Jurgensen *et al.* (1989, 1997) found conifer sapwood initially decayed by white-rot fungi, with a later change to brown-rot fungi, whilst the conifer-heartwood was solely decayed by brown-rot fungi (they found the angiosperm they studied primarily decayed by white-rot fungi).

BACTERIAL BREAKDOWN

Some species of bacteria are capable of degrading wood (Schink *et al.* 1981). Some bacteria are the only organisms other than the white-rots that are capable of degrading lignin (Blanchette 1995). Like soft-rot fungi, some bacteria are able to tolerate environmental conditions too extreme for white- and brown-rot fungi (Blanchette 1995). Bacteria and soft-rot fungi are often found together. However, Blanchette *et al.* (2004) only found soft-rot fungi decomposing the wooden huts left in Antarctica by the early explorers of the late 18th and early 19th centuries. This may be due to the requirement of the decomposers having to be imported into the environment with the wood, and the possible situation where suitable soft-rot fungal spores existed on the wood, but there were not suitable decomposition bacteria in the wood; and inoculation by bacteria could not occur due to the great distance from any suitable inoculation source.

MICRO-ORGANISM INOCULATION

Many fungal spores and decomposer bacteria are undoubtedly brought to the CWD piece by invertebrates (Leach *et al.* 1934; Harmon *et al.* 1986; Maser *et al.* 1988), as well as other animals scurrying about the forest floor. The tunnels of wood-boring invertebrates allow free-inoculation by wind-borne micro-organisms (Leach *et al.* 1937; Maser *et al.* 1988; Torres 1994). The greater the number of tunnels created by these invertebrate larvae, the greater the access afforded to the inner-wood of the tree, and the greater the inoculation by fungal spores (Leach *et al.* 1937); with a corresponding reduction in colonisation-time by the fungi. Many fungal spores would also be transported throughout the forest by wind. The entrance holes and galleries made by boring invertebrates afford decomposer organism entry to the wood interior much earlier than would be available by decomposition alone (Leach *et al.* 1937; Ausmus 1977; Maser *et al.* 1988).

2.1.2.2 Discussion of Microbial Breakdown of CWD

Fungi and bacteria are major decomposers of wood in the terrestrial environment (Graham 1925; Savely 1939; Gonor et al. 1988). Savely (1939) suspected that fungi were the major decomposer organisms of CWD creating a succession of different habitats within the wood. Preliminary species modify the wood to a condition that is favourable for succeeding species (Graham 1925).

All groups of CWD decaying fungi and bacteria utilise the cellulose and hemicellulose of CWD, but only the white-rot fungi and bacteria are able to degrade lignin structurally (see Table 2-1).

Table 2-1. The different decomposer organisms and the structures they degrade during CWD decomposition.

FUNGI	DIVISION	DEGRADES		
		Lignin	Cellulose	Hemicellulose
White-rot	**Basidiomycota**	✓	✓	✓
Brown-rot	**Basidiomycota**	**Modifies, but leaves structurally intact**	✓	✓
Soft-rot	**Ascomycota**	×	✓	✓
	Deuteromycota	×	✓	✓
Bacteria	—	✓	✓	✓

The white- and brown-rots are the major decomposers of CWD (Swift 1977). This makes the lignin-degrading white-rots the most important organisms in respect to CWD decomposition (Madigan *et al.* 1997). Soft-rot fungi and bacteria are better tolerators of extreme environmental conditions, and dominate over the white-rot and brown-rot fungi in harsh environments. In extreme environments, where only soft-rots and bacteria can exist, bacteria are the sole degraders of CWD lignin. Soft-rot fungi are not found in hyper-extreme environmental conditions, and bacteria are the only degraders of wood in these environments. For example, saturated wood with high extractive concentration and low O_2 concentration is only degraded by bacteria (Blanchette 1995). All fungi require oxygen, and are incapable of colonising CWD in anaerobic environments (Blanchette 1995). Waterlogged CWD are primarily decomposed by bacteria (Blanchette 1995).

High tannin and resin concentrations in some CWD provide resistance to fungal colonisation, and cause a corresponding decrease in decay rates over CWD with lower concentrations (Blanchette *et al.* 2004).

The total quantity of products produced by fungi is a reflection of the amount of decaying wood available, and the range of products produced by the fungi is a reflection of the amount of wood in different stages of decay, with greater species richness leading to a greater range of products produced (Temnuhin 1996).

Soft-rots and bacteria are better stress tolerators than the white- and brown-rots, while the white- and brown-rots are better competitors when conditions are benign. An overall diagram of the interaction of CWD decomposer organisms with the environments they occur in can be seen in Figure 2-2.

Termites are important decomposer organisms in some ecosystems (Harmon *et al.* 1987; Moorhead and Reynolds 1991; Torres 1994). The extent of wood excavation by termites also affects calculated decay rates (Woldendorp *et al.* 2002a, b). Termite action may appear to be a form of fragmentation (particle removal), but it can also be thought of as a form of natural decomposition, as the wood particles are metabolised by micro-flora (e.g. protists) in the termite gut and excreted *in situ* (Maser *et al.* 1988; Eggleton *et al.* 1997). Some soil-resident protists are also decomposers of CWD in contact with the soil surface as well as wood incorporated into the mineral soil (Adl and Gupta 2006).

Despite fungi being the major focus on wood degradation, due to its impact on commercial timber, the contribution of the inconspicuous bacteria to CWD-decay must

not be disregarded, and their contribution to the breakdown of woody material may equal, or even surpass, that of the fungi.

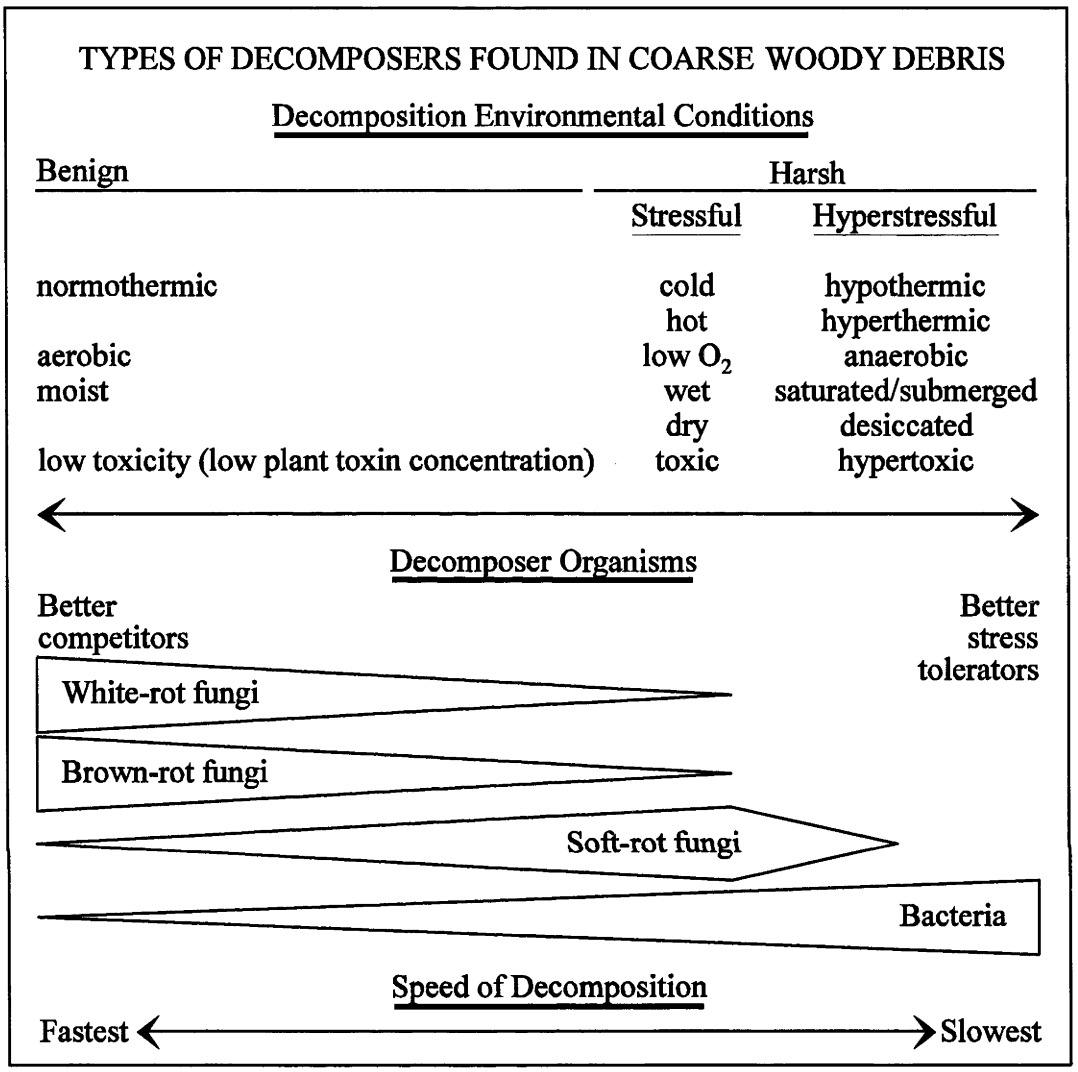


Figure 2-2. A generalised view of the decomposer organisms responsible for the decay of CWD under varying environmental conditions.

2.1.3 ORIENTATION BIAS OF CWD

Orientation bias has often been considered troublesome for field surveys of CWD. This has led to methods being developed to account for orientation bias when it is suspected of potentially biasing the CWD survey results. (See section 2.2.6.1 *Plot-Based Vs. Line-Intersect Surveys* for a discussion of the methods used to account for orientation bias in field surveys.)

2.1.3.1 Causes of Orientation Bias

WINDTHROW

In a study of SDT breakage in the northern Swiss Alps, Albisetti *et al.* (2003) found that the general direction of CWD orientation corresponded with the predominant wind direction, despite the sites being on highly sloping ground (13-35°).

SLOPE

Slope would be expected to be a source of orientation bias on steep-sloping terrain, where a greater proportion of the CWD could be expected to be oriented downslope (in the direction of aspect). However, slope generally does not appear to have an affect on CWD orientation. The non-affect of slope may be due to windthrow having a greater affect than slope, as most SDTs and living trees may fall during periods of high wind, with relatively few SDTs falling during periods of calm weather.

2.1.4 NUTRIENT CYCLING

CWD forms a major component of a forest's nutrient storage (Fogel and Cromack 1977; Maser *et al.* 1988; Hendrickson 1988; Spies and Cline 1988; Schowalter 1992; Schowalter *et al.* 1998; Spetich *et al.* 1999; Brown *et al.* 2003), and its decomposition plays a critical role in regulating the release of sequestered nutrients back to the forest ecosystem (Fogel and Cromack 1977; Fahey 1983; Schowalter 1998; Chojnacky and Heath 2002). Understanding the nutrient dynamics of CWD will allow a more accurate assessment of the critical role of CWD in nutrient cycling (Idol *et al.* 2001), and allow for better management of this important component of the forest environment.

In this thesis, nutrients will be discussed in brief and general terms only. However, due to the volatile nature of nitrogen, making it a highly-variable and fleeting resource, a proportionately larger discussion is given to the cycling and fixation of nitrogen in CWD.

2.1.4.1 Nitrogen (N)

Nitrogen is usually the element of major concern in forest nutrient dynamics (Tabak and Cooke 1968; Bormann *et al.* 1977; Adams and Attiwill 1984; Means *et al.* 1992), as it is important for protein synthesis and plant growth (Knox *et al.* 1995; Crews 1999). Nitrogen is used by plants for the manufacture of proteins, alkaloids, and many other important cellular compounds (Cowling and Merrill 1966; Tabak and Cooke 1968).

Nitrogen in CWD is important due to N often being limiting to organism-growth, and therefore restrictive in ecosystem functioning and productivity (Bormann *et al.* 1977; Moorhead and Reynolds 1991; Vitousek and Howarth 1991; Knox *et al.* 1995; Crews 1999; Brown *et al.* 2003; Bütler *et al.* 2007). Some studies (e.g. Merrill and Cowling 1965, 1966a, b; Ausmus 1977; Spano *et al.* 1982) have found nitrogen-concentration to be a major factor in controlling the decay-rate of CWD.

Nitrogen concentrations of CWD generally increase during decomposition for both conifers (see Grier 1978; Foster and Lang 1982; Graham and Cormack 1982; Harmon *et al.* 1987; Means *et al.* 1992; Chee 1999; Rose 2000; Currie and Nadelhoffer 2002; Bütler *et al.* 2007) and angiosperms (see Torres 1994; Schowalter *et al.* 1998; Chee 1999; Idol *et al.* 2001; Currie and Nadelhoffer 2002). Schowalter *et al.* (1998) and Idol *et al.* (2001) did find N increasing in *Quercus* CWD during decay only to decrease later. Means *et al.* (1992) found a contrary trend with decreasing N concentrations during the decomposition of the conifer *P. menziesii*.

In the literature, percentage N concentrations range from a maximum of 1.360% (Currie and Nadelhoffer 2002; *P. resinosa* conifer) to a minimum of 0.041% (Bütler *et al.* 2007; *P. abies* conifer). Actual N concentrations range from a maximum of 3.213 mg cm^{-3} (Currie and Nadelhoffer 2002; mixed angiosperm*) to a minimum of 0.123 mg cm^{-3} (Alban and Pastor 1993; *P. glauca* conifer†).

ACCUMULATION

INTRODUCTION. The struggle for trees to grow and persist in N-limited environments has led to the efficient recycling of N within the wood of the living tree (Merrill and Cowling 1966b), resulting in older wood (the heartwood) being low in N concentration, making it a poor food source (Cowling and Merrill 1966; Merrill and Cowling 1966a, b; Aho *et al.* 1974), consequently CWD has low N-concentrations (Spano *et al.* 1982). Merrill and Cowling (1966a, b) found angiosperms to have higher heartwood N-concentrations than conifers.

Many studies have found N-concentrations increasing during the decomposition of woody debris; such studies include Gosz *et al.* (1973), Grier (1978), Lambert *et al.* (1980), Melillo *et al.* (1982), Foster and Lang (1982), Fahey (1983), Barber and Van Lear (1984), Jurgensen *et al.* (1987), Arthur *et al.* (1993), Alban and Pastor (1993),

Footnotes
* Calculated from percent of wood density provided.
† Calculated from percent of wood density provided.

Busse (1994), Schowalter *et al.* (1998), Laiho and Prescott (1999), Idol *et al.* (2001), and Currie and Nadelhoffer (2002). An increase in N-concentration is ecologically important, as it is likely to cause an increase in the decomposer-community, with a concomitant increase in decay rate, of N-deficient material (Parnas 1975), and eucalypt woody debris, such as CWD, is generally N-deficient (Ashton 1975).

CWD N INPUTS — DYNAMICS. Edmonds *et al.* (1986) found that bark had higher N concentrations than wood in *P. menziesii* (a conifer) and *A. rubra* (an angiosperm) in newly felled trees. This higher N concentration in the bark may encourage decomposer organisms to colonise the new CWD, where they then infect the wood under the bark. Indeed, some of the increase in the N content of the wood, during decomposition, may be N translocated from the bark to the wood. It may be interesting to learn whether newly-formed CWD, of comparable ages, has different decomposer infection rates for samples with bark and samples with the bark removed. Edmonds *et al.* (1986), in a study of *P. menziesii* (a conifer) and *A. rubra* (an angiosperm) also found that larger-diameter CWD had a lower N concentration than smaller-diameter CWD; this may be due to the lower proportion of mass accounted for by bark in the larger diameter wood. Correspondingly, Stewart and Flinn (1985) also found that larger-diameter *Eucalyptus* L'Hér. CWD had lower nutrient concentrations.

CWD N INPUTS — SOURCES AND AMOUNTS. Increasing N content, with increasing decay, may be the result of N seeding by rainfall, leaching of N from covering litter by rainfall, long distance translocation into the CWD from the soil and forest floor by fungal hyphae, through non-symbiotic fixation by bacteria, crown/canopy wash, and insect frass (Cowling and Merrill 1966; Merrill and Cowling 1966a; Gosz *et al.* 1973; Grier 1978; Granhall and Lindberg 1980; Melillo *et al.* 1982; Silvester *et al.* 1982; Fahey 1983; Baker and Attiwill 1985; Adams and Attiwill 1986; Harmon *et al.* 1986; Jurgensen *et al.* 1987; Maser *et al.* 1988; Schimel and Firestone 1989; Alban and Pastor 1993; Hafner and Groffman 2005; Bütler *et al.* 2007). Exterior cracking of the CWD piece can trap litter and crown-wash (water falling from the leaves and branches of the crowns of standing trees), effectively creating a trap, which enhances the absorption of nitrogen released from the decaying-litter and crown-wash (Grier 1978; Silvester *et al.* 1982; Maser *et al.* 1988). Crown-wash (or canopy-wash) can be in the form of rain, snow, and dew/fog (Maser *et al.* 1988). It must be mentioned, that some of the N in crown-wash may be derived from cyanobacteria resident on the branches and leaves of the crown.

Fungi decay CWD faster when they have access to higher N concentrations from the surrounding environment, as occurs when the CWD is in contact with the ground, as this is used to supplement the meagre N available in wood Cowling and Merrill (1966).

Some N may also be imported by fungal hyphae to the bark, as most fungi would infect the CWD through the exposed outer surface; this may explain, to some degree, the higher N-concentrations found in the bark by Edmonds *et al.* (1986). Wells and Boddy (1990) and Wells *et al.* (1990) have shown translocation by fungi takes place with phosphorus, and, therefore, it is reasonable to expect that some N-translocation would also occur with fungi. Translocation of N from the forest floor into CWD may be a major source of N input into CWD (Fahey 1983; Hafner and Groffman 2005; Bütler *et al.* 2007).

CWD N INPUTS — N_2-FIXATION; INTRODUCTION. When discussing nitrogen fixation in this thesis, it is inferred that the discussion concerns the fixation of atmospheric N_2; consequently, N-fixation is actually referring to N_2-fixation. Hardy *et al.* (1973) and Granhall and Lindberg (1980) provide reviews of N_2-fixation.

Nitrogen-fixation by decomposer organisms is important for forest N-cycles (Larsen *et al.* 1978; Hendrickson 1988). The importation of nitrogen into CWD, and *in situ* N_2-fixation (Larsen *et al.* 1978; Hendrickson 1991; Kraus *et al.* 2003), encourages colonisation and growth of decomposer organisms that do not fix their own N_2, leading to an increased decomposition rate in CWD that is N-limited (Findlay 1934; Larsen *et al.* 1978; Roskoski 1980; Schink *et al.* 1981; Silvester *et al.* 1982; Jurgensen *et al.* 1984, 1987, 1989; O'Connell and Grove 1987; Nuntagij *et al.* 1989; Hendrickson 1991; Blanchette *et al.* 2004). Different species of trees provide CWD-habitat for different species of N_2-fixing bacteria (Hendrickson 1991), affording heterogeneity of N_2-fixation rates, which, to some extent, would account for some of the heterogeneity of decomposition-rates among species (Hendrickson 1988; Jurgensen *et al.* 1989).

Nitrogen "fixation" by decomposer fungi was detected by Larsen *et al.* (1978), but this was due to metabolic-denaturing and recycling of existing N-compounds, and not fixation of atmospheric-N_2. Many wood-decaying fungi are associated with N_2-fixing bacteria (Aho *et al.* 1974), which may have contributed to the erroneous interpretation that these fungi were fixing N_2, when in fact is was the bacteria associated with the fungi that were fixing the N_2. This association of decay-fungi with N_2-fixing bacteria suggests that fungi are more vigorous in growth nearer the source of higher N-concentrations, which, in turn, suggests that the presence and concentration of

N_2-fixing bacteria indirectly influences the potential decomposition rate of the wood-substrate. Currently, there is not any evidence that any fungi can fix atmospheric-N_2, and it is assumed that all fixation of atmospheric-N_2 is done by bacteria. Tabak and Cooke (1968) provide an extensive review of early fungi research, and some of the misinterpretations erroneously attributing N_2-fixation to fungi.

In the literature, the terms 'symbiotic nitrogen fixation' and 'non-symbiotic nitrogen fixation' are used extensively. Symbiotic nitrogen fixation refers to the N_2-fixation between symbiotic soil bacteria and plants, such as occurs in regenerating forests between *Acacia* Mill. and the N_2-fixing bacterium *Rhizobium* Frank. (There are many other symbiotic relationships between other legumes and non-legumes with N_2-fixing bacteria.) Symbiotic N_2-fixation can also occur between N_2-fixing bacteria and other organisms such as fungi (in lichens), hornworts, and liverworts (Knox *et al.* 1995; Adams 2002). Non-symbiotic nitrogen fixation refers to the fixation of atmospheric-N_2 by free-living heterotrophic and autotrophic bacteria.

N_2-fixation by heterotrophic bacteria generally occurs in anaerobic or near-anaerobic conditions (Aho *et al.* 1974; Roskoski 1980; Schink *et al.* 1981; Spano *et al.* 1982; Jurgensen *et al.* 1989; Kravchenko and Doroshenko 2003), as nitrogenase is inactivated by the presence of O_2 (Haystead *et al.* 1970; Hardy *et al.* 1973; Li *et al.* 1992; Hicks *et al.* 2003). Both facultative and obligate anaerobic N_2-fixing bacteria are found in CWD (Aho *et al.* 1974; Schink *et al.* 1981; Spano *et al.* 1982).

Sharp and Millbank (1973) showed that heterotrophic N_2-fixing bacteria can colonise wood from the surrounding soil; apparently via tracheids and vessels. Seidler *et al.* (1972) found N_2-fixing heterotrophic bacteria in the wood of some living trees of NW North America; the species were each associated with specific fungi. Baker *et al.* (1983) found N_2-fixation by heterotrophic bacteria in submerged wood.

The fixation of atmospheric-nitrogen (N_2) results in the manufacture of ammonia (NH_3) (Dilworth 1966; Hardy *et al.* 1968; Bergersen 1970), which is readily protonated to ammonium (NH_4^+) that will eventually become available for plant growth (Granhall and Lindberg 1980; Crews 1999); the reaction is: NH_3 (aq) + H^+ (aq) $\rightarrow$ NH_4^+ (aq). Upon the death of the N_2-fixing bacteria, the released NH_4^+ is nitrified, by nitrifying bacteria, to NO_3^- (nitrate) via the intermediate NO_2^- (nitrite), which is then available for use by decomposer organisms in the CWD-piece and by primary-producer organisms when leached from the CWD-piece (Knox *et al.* 1995; Attiwill *et al.* 1996; Crews 1999).

CWD N INPUTS — N_2-FIXATION; HISTORY AND ASSAY METHODS. There have been several methods used to assay nitrogen. The three most common are discussed below.

The Kjeldahl and Dumas methods of N-concentration determination do not distinguish between fixed and non-fixed sources of N, and is time-consuming (Hardy *et al.* 1968, 1973), making it effective for determining N-concentration, but not useful for assaying N sourced from N_2-fixation.

The majority of N_2 in the atmosphere is ^{14}N, with ^{15}N being relatively rare; the naturally-occurring atmospheric ratio of ^{14}N:^{15}N is 272:1 (Coplen *et al.* 1992). Studies of atmospheric-nitrogen uptake, usually involve increasing the proportion of ^{15}N in the artificial atmosphere surrounding the substrate containing the N_2-fixing bacteria. A lowering of the ^{14}N:^{15}N ratio within the organism is evidence of N_2-fixation during the experiment.

$^{15}N_2$ isotope-analyses only assesses N_2-intake, it does not include other sources of N (Hardy *et al.* 1973).

Hardy *et al.* (1973) claim that $^{15}N_2$ mass-spectrometry analysis is 1000 times more as sensitive than the Kjeldahl method.

Disadvantages of the $^{15}N_2$ assay-method include high expense, a lot of equipment required, and insensitive to the low concentrations often encountered with field samples (Hardy *et al.* 1973). $^{13}N_2$ radioactive isotope-analyses are more sensitive to low concentrations than $^{15}N_2$ analysis, but are more expensive, require even more equipment, and have inherent analytical problems caused by the short half-life of $^{13}N_2$ (Hardy *et al.* 1973).

Use of the acetylene-reduction technique/method (ART) in determining atmospheric N_2-fixation has become widespread (Spano *et al.* 1982). The nitrogenase-enzyme found in N_2-fixing bacteria not only fixes atmospheric-N_2, but also reduces acetylene to ethylene ($C_2H_2 \rightarrow C_2H_4$), as well as other reactions (Dilworth 1966; Hardy *et al.* 1968, 1973). The reduction is from the alkyne (triple carbon-carbon bonded; C≡C) C_2H_2 to the alkene (double carbon-carbon bonded; C=C) C_2H_4, effectively reducing the triple carbon-carbon bond to a double carbon-carbon bond (McMurry 1996); this is a 1:1 conversion. Nitrogenase reduces C_2H_2 to C_2H_4 only, it does not reduce the C_2H_4 to any other compound, nor do the N_2-fixing bacteria produce C_2H_4 from any source other than C_2H_2 (Hardy *et al.* 1968). Nitrogenase is the only enzyme known to reduce C_2H_2 to C_2H_4 (Witty 1970). The C_2H_4 end-product does not interfere with nitrogenase function,

and this is why C_2H_4 is the end-product of C_2H_2 reduction (Dilworth 1966). Nitrogen-fixation, as N_2, and the associated acetylene-reduction, by nitrogenase, only occur when nitrogen is limiting (Dilworth 1966; Hardy *et al.* 1968).

The ART is more sensitive than N-isotope analyses (Hardy *et al.* 1968, 1973). However, the requirement for careful handling of the flammable/explosive C_2H_2 is an important consideration when planning to use the ART. The ART has an inherent disadvantage in that it is an indirect method of assessing N_2-fixation (Hardy *et al.* 1968).

During experimental-assays of N_2-fixation, light, temperature, moisture-level, and pO_2 (oxygen partial-pressure), must mimic the field conditions for the laboratory-assay to be valid (Bergersen 1970; Hardy *et al.* 1973). Errors in N_2-fixation assays are especially sensitive to unmatched pO_2 between the laboratory-assay and the field-conditions (Bergersen 1970). Witty (1970) also found that any O_2 in the experimental-controls can oxidise C_2H_4 produced by nitrogenase-activity, whilst the C_2H_2 added to the treatment-samples inhibits oxidation. This has the effect of artificially reducing oxidation of the C_2H_4 produced in the treatments, giving the impression that the treatment-effects are greater than is actually the case. Witty (1970) cautions against this source of overestimation of increased nitrogenase-activity, by suggesting that controls be subjected to an anaerobic atmosphere to reduce oxidation of the nitrogenase-produced C_2H_4. Nitrogenase activity has also been found to decrease with lower temperatures (Hardy *et al.* 1968). Hendrickson (1988) discusses some other problems/considerations with the ART.

Hardy *et al.* 1968 found an acetylene-reduction:N_2-fixed ratio range of 3.7 to 4.2, which they interpreted as being in the range of 3 to 4.5. In a review of non-symbiotic N_2-fixation, Hardy *et al.* (1973) found a range of acetylene-reduction ratios from 1.5:1 to 8.6:1 (from Table 2 of Hardy *et al.* 1973), and Liengen (1999) found ratios from 0.022 to 4.88 for N_2-fixation in Arctic cyanobacteria. The theoretical ratio of $C_2H_2 \rightarrow C_2H_4$: N_2-fixed is 1.5:1 (Bergersen 1970). However, as acetylene (C_2H_2) inhibits nitrogenase activity (Dilworth 1966; Hardy *et al.* 1968) this ratio would change as the concentration of C_2H_2 changes; with initial high values of C_2H_2, which inhibit N_2-fixation, resulting in a high ratio, with the ratio decreasing as the concentration of the inhibiting-C_2H_2 is decreased, allowing more N_2-fixation. Consequently, this ratio not only will vary depending on initial conditions when nitrogenase is produced by the bacterial-cell, but will decrease as the inhibiting-C_2H_2 is reduced (to C_2H_4) and the N_2-fixation is increased. This expected decrease-over-time of the $C_2H_2 \rightarrow C_2H_4$:

N_2-fixed ratio was clearly demonstrated by Bergersen (1970). Extracting values from Figure 5 of Bergersen (1970) shows a decrease in the ratio from a maximum of 2.7:1 after 2 hours to a minimum of 0.1:1 after 20 hours. In fact, Bergersen (1970) found that the C_2H_2 decreased before N_2-fixation increased, corresponding with the expected pattern, and agreeing with their postulation of increasing efficiency over time.

Some investigators (e.g. Cornaby and Waide 1973; O'Connell *et al.* 1979; Jurgensen *et al.* 1987; O'Connell and Grove 1987; Li *et al.* 1992) have assumed a $C_2H_2 \rightarrow C_2H_4$: N_2-fixed ratio of 3:1, and this has generally been attributed to Hardy *et al.* (1968). (Li *et al.* (1992) did not state that they used the 3:1 ratio, but back-calculating their C_2H_2-reduced and N_2-fixed calculations show that a 3:1 ratio was used.) However, as state above, Hardy *et al.* (1968) found a ratio-range of 3.7-4.2, and there is not a recommendation by the authors to use a ratio of 3:1; it is rather mystifying how this 'recommendation' has arisen. Due to high natural variation in the $C_2H_2 \rightarrow C_2H_4$: N_2-fixed ratio, the 3:1 ratio cannot be assumed to be a valid 'standard' (Bergersen 1970). Hicks *et al.* (2003) found the $C_2H_2 \rightarrow C_2H_4$: N_2-fixed ratio to be affected by assay-temperature and wood-species. Roskoski (1981) and Silvester *et al.* (1982) found the ratio changed with length of experiment, which is to be expected due to the inhibitory affects of C_2H_2 on N_2-fixation by nitrogenase; consequently, length of experiment must be considered, and there may be a need for some form of standardisation for length of experimentation with the ART. To determine the exact amount of N_2-fixed in any given experiment, the $C_2H_2 \rightarrow C_2H_4$: N_2-fixed ratio must be determined for every condition for which field-calculations are to be made Bergersen (1970).

The indirect nature of the assessing N_2-fixation by the ART (Hardy *et al.* 1968) exposes the method to errors when assumptions are made to the C_2H_2:N_2 ratio. As acceptance of a low ratio-value (e.g. such as 3:1) will lead to overestimations of the actual N_2-fixation amount/rate if the actual ratio is greater (Witty 1970; Hendrickson 1988). Great caution should be exercised if deciding to use the 3:1 ratio (O'Connell and Grove 1987), as it is very unlikely that this assumed-ratio accurately reflects the actual-ratio occurring in the ecosystem (Witty 1970). See Bergersen (1970), Roskoski (1981), and Silvester *et al.* (1982) for a discussion on the problems related to the 3:1 conversion-ratio of moles C_2H_2 reduced (to C_2H_4) to moles N_2 fixed.

The nitrogenase-enzyme is deactivated by exposure to O_2 (Li *et al.* 1992; Hicks *et al.* 2003). Consequently, exposure to air deactivates the nitrogenase-enzyme; the

inactivation is reversible after short exposures to low O_2-concentrations, but is irreversible after longer (e.g. 5 minutes or more) exposures or exposure to moderate-or-high concentrations of O_2 (Haystead *et al.* 1970; Hardy *et al.* 1973). Silvester *et al.* (1982) found that N_2-fixation increased as O_2 concentration was decreased below that of atmospheric O_2. Savely (1939) found a concomitant increase in CO_2 and decrease in O_2 in decomposing *Pinus* and *Quercus* logs. Consequently, due to the depletion of O_2 during CWD-decomposition creating a microaerophilic environment, due to the respiration of the resident heterotrophic organisms (Jurgensen *et al.* 1989; Schink *et al.* 1981; Li *et al.* 1992), it is to be expected that local-atmosphere conditions favourable for N_2-fixation will become more apparent as decomposition proceeds. This changing toward a less-oxidative atmosphere is closely linked to the water-relations of the environment within the log; the higher the water-content, the slower the diffusion of gases between the inner-log and the atmosphere (see 2.1.1.3 for further discussion on this point).

The O_2-deactivation of nitrogenase makes laboratory assays cumbersome, as anoxic conditions must be ensured at all times; even the slightest O_2 contamination above the predetermined experimental-concentration will result in erroneously-lowered nitrogenase activity. Of course, the bacteria that fix N_2 can be aerobic or anaerobic, but the site of N_2-fixation within the bacterial-cell must be anaerobic. Aerobic N_2-fixing facultative-bacteria can create locally near-anoxic conditions, suitable for nitrogenase-activity, by increasing metabolism (Hicks *et al.* 2003).

Carbon monoxide (CO) inhibits nitrogenase activity; limiting both N_2-fixation and acetylene-reduction (Dilworth 1966; Hardy *et al.* 1968, 1973). As mentioned above, acetylene also inhibits nitrogenase activity (Dilworth 1966; Hardy *et al.* 1968).

Irreversible deactivation of nitrogenase by O_2 does not cause irreversible harm to the bacterium, as it will manufacture more nitrogenase once conditions are favourable.

CWD N INPUTS — N_2-FIXATION; OCCURRENCE. Nitrogen fixation occurs in CWD (Cornaby and Waide 1973; Granhall and Lindberg 1980; Silvester *et al.* 1982; Vitousek and Matson 1984; Hendrickson 1991; Li *et al.* 1992; Hicks *et al.* 2003; Pérez *et al.* 2004), which makes CWD an ecologically-important N_2-fixation media (Granhall and Lindberg 1980), despite being understudied (Hicks *et al.* 2003). Consequently, much of the N-accumulation in CWD, as it decomposes, is due to the action of N_2-fixing bacteria (Graham and Cromack 1982; Vitousek and Matson 1984). Due to this presence of N_2-fixing bacteria in CWD, higher quantities of CWD should enhance ecosystem

N_2-fixation (Pérez *et al.* 2004). Indeed, Cornaby and Waide (1973) found that N_2-fixation in *Castanea dentata* (Marsh.) Borkh. CWD was higher than that of the surrounding soil.

The heterotrophic and autotrophic N_2-fixing bacteria are often referred to as "diazotrophs" (Silvester *et al.* 1982).

CWD N INPUTS — N_2-FIXATION; AMOUNTS & DYNAMICS. The major natural sources of ecosystem nitrogen-import include N_2-fixation, nitrogen present in rainfall, and atmospheric nitrogen-deposition (Jurgensen *et al.* 1987).

In a central Sweden conifer-forest study of N_2-fixation, Granhall and Lindberg (1980) found that N_2-fixation in CWD and stumps accounted for 10-39% of total site N_2-fixation (calculations made from data of their Figure 1).

Roskoski (1980), Jurgensen *et al.* (1989), Liengen (1999), and Zackrisson *et al.* (2004) found bacterial N_2-fixation increased with temperature increase; whereby summer N_2-fixation was greater than winter fixation. Jurgensen *et al.* (1980) found that N_2-fixation by heterotrophic CWD-inhabiting bacteria was greater during warmer weather (higher at 15.8°C than at 13.2°C). This is to be expected, as metabolism is positively correlated with heat availability, affording greater N_2-fixing rates at higher temperatures. (See 2.1.1.3 for further discussion of affects of temperature).

Spano *et al.* (1982) and Jurgensen *et al.* (1984, 1987) found that the rate of bacterial N_2-fixation increased during decay of CWD, corresponding with increasing moisture content; although it must be mentioned that Hicks *et al.* (2003) found peak N_2-fixation occurred in the intermediate stages of decay, followed by a slight decrease. N_2-fixation by facultative-anaerobic bacteria is more likely to occur in CWD, where high moisture contents can create a near-anaerobic environment, than other litter components or surface soil where aerobic conditions occur (Roskoski 1980; Spano *et al.* 1982; Jurgensen *et al.* 1987). Saturated wood allows some measure of anoxia (Boddy 1983a) due to reduced diffusion of gases in the vessels and tracheids (Boddy 1983b); the length of the CWD-piece also affects gas-diffusion as longer-logs have a higher resistance for gas-exchange with the atmosphere (Boddy 1983b). Of course, if the high moisture content restricts the transfer of O_2 from the external environment to the high-moisture environment of the inner log, it must also be assumed that this same high-moisture content must also restrict the flow of N_2 from the external environment to the inner log where the N_2-fixing bacteria reside. However, despite the restricted flow of O_2 and N_2 from the external environment (where the normal atmospheric partial-pressures of O_2

and N_2 are higher than within the 'wet' inner-log), there would, nevertheless, be some flow into the inner log environment. The inflowing O_2 would be rapidly absorbed by the heterotrophic bacteria and fungi, but the N_2 would remain free for use by the N_2-fixing bacteria. Jurgensen *et al.* (1984) found a curvilinear-relationship between CWD moisture content and rate of N_2-fixation, showing the importance of high moisture-content to N_2-fixation rate within CWD. Moisture-content is the major environmental factor influencing N_2-fixation in CWD (Hendrickson 1988); O'Connell and Grove (1987) found moisture-content also had a greater influence than temperature in determining N_2-fixation rates in fine litter of Australian eucalypt forests.

CYANOBACTERIA. Some of the non-symbiotic fixation of atmospheric N_2 would undoubtedly be the result of nitrogen fixation by cyanobacteria residing on the surface of the CWD. While there are no reports of cyanobacteria on CWD, they have been reported in soil (e.g. Granhall and Lindberg 1980; Harper and Pendleton 1993; Widmer *et al.* 1999; Mishra and Dhar 2004; Zackrisson *et al.* 2004) and on leaves in the canopy of forests (e.g. Matzek and Vitousek 2003). Forest cyanobacteria occur as free-living species, as well as symbionts with moss and lichens (Bergstrom and Tweedie 1998; Saxena and Harinder 2004), and would occur in all forms on the surface of CWD. Invertebrates and other small scurrying animals would undoubtedly transport cyanobacteria from the forest floor and canopy to the CWD surface.

Cyanobacteria are photosynthetic bacteria, they are often mistakenly referred to as 'blue-green algae'; cyanobacteria are prokaryotes, and, as such, are not members of the eukaryotic algae. (Additionally, cyanobacteria only possess chlorophyll-*a*, whereas green algae possess chlorophyll-*a* and chlorophyll-*b*.) Cyanobacteria fix atmospheric N_2 (Vitousek and Howarth 1991; Knox *et al.* 1995; Liengen 1999; Paulsrud 2001; Tsavkelova *et al.* 2003a, b; Zackrisson *et al.* 2004), as well as reduce C_2H_2 to C_2H_4 like heterotrophic N_2-fixing bacteria (Hardy *et al.* 1968). Nitrogen-fixation occurs in members of the heterocystous and non-heterocystous cyanobacteria, and in both filamentous and coccoid cyanobacteria (Wyatt and Silvey 1969; Haystead *et al.* 1970; Hardy *et al.* 1973). As is to be expected with photosynthetic organisms, N_2-fixation by cyanobacteria is affected by light conditions (Granhall and Lindberg 1980).

The consistently higher bark N-concentrations found by Edmonds *et al.* (1986) somewhat support the hypothesis that cyanobacteria may be contributing to some of the N accumulation in CWD. As far as cyanobacterial N_2-fixation is concerned, smaller-diameter logs have a greater surface-area:volume ratio, that may afford a greater

input-concentration of N (Hendrickson 1991), but this would be somewhat offset by the smaller-diameter affording a faster leaching-rate.

Cyanobacteria can be free-living or found in symbiotic relationships with many other organisms. Cyanobacteria occur in symbiotic relationships with moss (Granhall and Lindberg 1980; Zackrisson *et al.* 2004); Granhall and Lindberg (1980) found the cyanobacterium *Nostoc* Vaucher ex Bornet & Flahault occurred endosymbiotically within the hyaline-cells of *Sphagnum* L. moss, but did not occur epiphytically, whilst Zackrisson *et al.* (2004) found the N_2-fixing cyanobacterial-symbiont growing epiphytically on the moss *Pleurozium schreberi* (Bird.) Mitt.. Cyanobacteria also occur in symbiotic relationships with some liverworts and hornworts (Adams 2002), and with the angiosperm genus *Gunnera* (Bonnett and Silvester 1981). Lichens are a symbiotic relationship between fungi and either a cyanobacterium, chlorophyte, or xanthophyte (Knox *et al.* 1995; Tsavkelova *et al.* 2003a, b). Often the cyanobacterial-symbiont in lichen is of the genus *Nostoc* (Paulsrud 2001). Some lichens fix atmospheric-nitrogen (N_2) (Granhall and Lindberg 1980; Maser *et al.* 1988; Norby and Sigal 1989), and this is due to the actions of the cyanobacterial-symbiont. Roskoski (1980) suggest that lichens may be important in ecosystem N_2-fixation.

The presence of cyanobacteria in the canopy of forest trees has allowed epiphytic orchids to form a symbiotic relationship with cyanobacteria, with the cyanobacteria infecting the roots of the epiphytic orchids (Tsavkelova *et al.* 2003a, b). The presence of cyanobacteria in the litter-layer and soil surface allows inoculation of cyanobacteria into the coralloid roots of some cycads, she-oaks, and alder (Halliday and Pate 1976; Grove *et al.* 1980; Knox *et al.* 1995). It is likely that N_2-fixation by cyanobacteria is much more important in terrestrial ecosystems than has generally been assumed (Hobbie *et al.* 2002).

DISCUSSION OF N-ACCUMULATION. Fungal N_2-fixation in decomposing wood has long been postulated (e.g., Merrill and Cowling 1966a), but this is a case of N-recycling, and not fixation of atmospheric-N_2, as occurs with N_2-fixing bacteria. Indeed, as Tabak and Cooke (1968) explain, many early investigators mistook recycling of existing-nitrogen for N_2-fixation, often because of inadequacies in the Kjeldahl method of assaying N-content. It is now accepted that fungi cannot fix N_2, and it is bacteria, both free-living and symbiotic, that fix atmospheric nitrogen.

N DECREASE

Busse (1994) found the CWD N concentration increasing (over initial values) up to decay class four (of five decay classes). However, the N concentration decreased from Class 4 to Class 5. The author suggests a net N mineralisation (release to the soil) occurring between decay stages four and five. Alban and Pastor (1993) also found that N concentrations only decreased in the latter stages of CWD decay, where there was a net release of N to the forest environment. Alban and Pastor (1993) found that net N release to the environment was only achieved after 40-100 years for *P. tremuloides*, *P. glauca*, *P. resinosa*, and *P. banksiana*, while Lambert *et al.* (1980) found that net N release only occurred after 33 years of decomposition of *Abies balsamea* (L.) Mill. CWD. These findings suggest that there is a delay in the mineralisation of CWD N for several decades (Idol *et al.* 2001), if not longer.

N-DYNAMICS INCONCLUSIVE

Edmonds *et al.* (1986) found that *P. menziesii* and *A. rubra* trees had higher N concentrations in both wood and bark during winter, than in summer, with corresponding lower lignin:N and C:N ratios during winter. Consequently, CWD formed during winter will have higher N concentrations than CWD formed during summer. Therefore, it would seem that CWD formed during winter would likely have a higher initial decomposer infection and growth rate than CWD formed during summer. However, as mentioned earlier, Boddy and Swift (1984) and Edmonds *et al.* (1986) did not find any differences in decay rate due to seasonal differences in decay commencement.

2.1.4.2 Phosphorus (P)

Phosphorus concentrations of CWD have often been found to increase during decomposition for both conifers (see Foster and Lang 1982; Graham and Cromack 1982 — *Picea sitchens* (Bong.) Carr.; Means *et al.* 1992; Laiho and Prescott 1999; Bütler *et al.* 2007) and angiosperms (Torres 1994; Idol *et al.* 2001). However, Grier (1978) found P decreasing during CWD decomposition of the conifers *P. sitchens* and *T. heterophylla*, and Lambert *et al.* (1980) found an initial decrease followed by a stabilising of P concentrations in CWD of *A. balsamea* (conifer). Ganjegunte *et al.* (2004) found P remained stable during the first 13 years of decomposition of *Pinus radiata* D. Don (conifer) CWD. Arthur *et al.* (1993) found that P concentrations initially increased followed by a later decrease during the final stages of CWD

decomposition in a mixed angiosperm forest. Schowalter *et al.* (1998) found an initial decrease in the heartwood of *Quercus* spp. (angiosperm) followed by an increase in P concentration, but found a reverse-pattern in the sapwood of *Quercus* spp. (angiosperm) where P concentrations initially increased and then decreased. Fahey (1983; *Pinus contorta* var. *latifolia* Engelm. conifer), Barber and Van Lear (1984; *P. taeda* conifer), and Means *et al.* (1992; *P. menziesii* conifer) also found an initial increase in P concentration followed by a later decrease during decomposition of conifer CWD. These results show a high level of variability in phosphorus dynamics during the decomposition of CWD, however, there is a general trend of increasing P during CWD decomposition. Phosphorus dynamics during CWD decomposition show some similarity to the dynamics of nitrogen.

In the literature, percentage P concentrations range from a maximum of 0.460% (Idol *et al.* 2001; mixed angiosperm) to a minimum of 0.001% (Bütler *et al.* 2007; *P. abies* conifer). Actual P concentrations range from a maximum of 124 μg cm^{-3} (Schowalter *et al.* 1998; *Quercus* spp. angiosperm — calculated from percent of wood density provided) to a minimum of 4 μg cm^{-3} (Bütler *et al.* 2007; *P. abies* conifer).

Phosphorus is often limiting to organism growth (Bütler *et al.* 2007). Wells and Boddy (1990) and Wells *et al.* (1990) have shown translocation by fungi takes place with phosphorus, and, therefore, it is reasonable to expect that some P concentrations would increase during the decomposition of CWD.

2.1.4.3 Potassium (K)

Potassium concentrations of CWD have often been found to decrease in conifers during decomposition (see Grier 1978; Foster and Lang 1982; Graham and Cromack 1982 — *T. heterophylla*; Means *et al.* 1992; Arthur *et al.* 1993; Ganjegunte *et al.* 2004). However K has also been observed to remain constant, or at least inconclusive in respects to a trend, in some conifers (see Lambert *et al.* 1980; Graham and Cromack 1982 — *P. sitchens*). Schowalter *et al.* (1998) found CWD K concentration to increase in *Quercus* spp. (angiosperm) heartwood during decomposition, while the sapwood initially decreased and then increased. However, Idol *et al.* (2001), during CWD decomposition in a study of a mixed angiosperm forest, and Torres (1994) studying the angiosperm *Cyrilla racemiflora* L. in tropical rainforest, both found K to decrease during decomposition. The general trend is for K to decrease in conifer CWD during decomposition, but due to an inadequacy of information in the literature, angiosperm

K-dynamics cannot be generalised; although it probably does decrease as K is highly mobile and therefore easily leached (Torres 1994).

In the literature, percentage K concentrations range from a maximum of 0.240% (Gosz *et al.* 1973; *Acer saccharum* Marsh. angiosperm) to a minimum of 0.012% (Lambert *et al.* 1980; *A. balsamea* conifer). Actual K concentrations range from a maximum of 756 μg cm^{-3} (Schowalter *et al.* 1998; *Quercus* spp. angiosperm — calculated from percent of wood density provided) to a minimum of 35 μg cm^{-3} (Lambert *et al.* 1980; *A. balsamea* conifer — calculated from percent of wood density provided).

2.1.4.4 Calcium (Ca)

Calcium is generally regarded as being relatively immobile in decomposing CWD (Abbott and Crossley 1982; Brown *et al.* 1996), as it is embedded in the wood matrix (Abbott and Crossley 1982), which prevents it from being readily leached (Brown *et al.* 1996). However, Ca concentrations of CWD generally increase, albeit slightly, during decomposition for both conifers (see Foster and Lang 1982; Graham and Cromack 1982 — *P. sitchens*; Means *et al.* 1992; Arthur *et al.* 1993; Ganjegunte *et al.* 2004) and angiosperms (see Abbott and Crossley 1982; Torres 1994; Schowalter *et al.* 1998). Grier (1978) found an initial increase in Ca followed by a decrease during CWD decomposition of the conifer *P. sitchens*. Some investigations have found Ca to remain relatively stable in some conifer CWD during decomposition (see Lambert *et al.* 1980; Graham and Cromack 1982 — *T. heterophylla*). Idol *et al.* (2001) found Ca concentrations to decrease during CWD decomposition in a study of a mixed angiosperm forest.

In the literature, percentage Ca concentrations range from a maximum of 1.140% (Gosz *et al.* 1973; *Betula alleghaniensis* Brit. angiosperm) to a minimum of 0.065% (Lambert *et al.* 1980; *A. balsamea* conifer). Actual Ca concentrations range from a maximum of 3.190 mg cm^{-3} (Schowalter *et al.* 1998; *Quercus* spp. angiosperm — calculated from percent of wood density provided) to a minimum of 111 μg cm^{-3} (Lambert *et al.* 1980; *A. balsamea* conifer — calculated from percent of wood density provided).

Bark generally contains more Ca than the wood matrix, therefore, when samples of CWD contain bark, it is important to account for the contribution of bark to the amount of Ca in the sample (Abbott and Crossley 1982).

2.1.4.5 Magnesium (Mg)

Magnesium concentrations of CWD generally increase during decomposition of conifer CWD (see Grier 1978; Foster and Lang 1982 — *P. rubens*; Graham and Cromack 1982; Means *et al.* 1992). Foster and Lang (1982) found an initial increase in Mg concentration followed by a decrease during CWD decomposition of the conifer *A. balsamea*, yet Lambert *et al.* (1980) found Mg concentrations to remain constant during their study of *A. balsamea*. Ganjegunte *et al.* (2004) found Mg remained stable in the first 13 years of decomposition of *P. radiata* (conifer) CWD.

Arthur *et al.* (1993) found that Mg concentrations remained relatively stable during decomposition of CWD in a mixed angiosperm forest. Idol *et al.* (2001) found Mg decreased during decomposition of CWD in a *Quercus-Carya* (*Carya* L.) mixed angiosperm forest. Schowalter *et al.* (1998) found Mg concentrations to initially decrease and later increase during the decomposition of the sapwood of *Quercus* spp. (angiosperm), but the Mg dynamics of the heartwood decomposition were inconclusive. Torres (1994) found Mg concentrations to increase during decomposition of the tropical-rainforest angiosperm *C. racemiflora*. Unlike the conifers, angiosperm CWD decay does not show a general trend in Mg dynamics.

In the literature, percentage Mg concentrations range from a maximum of 0.100% (Gosz *et al.* 1973; *Fagus grandifolia* Ehrh. angiosperm) to a minimum of 0.008% (Foster and Lang 1982; *P. rubens* conifer). Actual Mg concentrations range from a maximum of 65 μg cm^{-3} (Lambert *et al.* 1980; *A. balsamea* conifer — calculated from percent of wood density provided) to a minimum of 17 μg cm^{-3} (Alban and Pastor 1993; *P. glauca* conifer — calculated from percent of wood density provided).

2.1.4.6 Sodium (Na)

Sodium concentrations of CWD generally increase during decomposition for both conifers and angiosperms; however, the dynamics of this increase are complex. A continuing Na increase, on conifer CWD, was found by Grier (1978), Lambert *et al.* (1980), and Graham and Cormack (1982 — *T. heterophylla*), and an initial increase in Na of conifer CWD followed by a later decrease was found by Foster and Lang (1982), Graham and Cromack (1982 — *P. sitchens*), and Means *et al.* (1992). Schowalter *et al.* (1998) found that Na concentrations initially increased followed by a later decrease during decomposition of *Quercus* spp. (angiosperm) sapwood and heartwood.

Sodium concentrations, from the literature, were not collected as part of this project, as many of the sites were close to oceanic-water, and this would confound any

within-ecosystem Na movement; consequently, Na literature-data was not collected for analyses.

2.1.4.7 Discussion

Some of the nutrients contained within CWD accumulate from external sources after tree death and fall. Nutrient leaching from litter lying on the upper surface of the fallen log is one source of nutrient input into the log (MacMillan 1981). Epiphytes, especially ferns with their relatively long fronds, also act as leaf-litter traps, accumulating litter on the CWD upper surface.

Many nutrients are also sourced internally from the CWD matrix by the action of colonising decomposer organisms. Blanchette (1995) found the white-rot genus *Ceriporiopsis* liberates Mn and Ca from the wood matrix, some of which is absorbed by the hyphae, and the rest left on the surface of the remaining wood. They suggested the liberated Mn and Ca, and possibly other cations, may lead to increased decomposition by other organisms. The generalisation by Blanchette (1995) is that some white-rot fungi cause a net release of available nutrients for use by other decomposer organisms.

Generally, N and P concentrations increase during CWD decomposition, only to be mineralised during the last phase of decomposition. Potassium is mineralised continually during decomposition, with a consistent steady release to the surrounding environment. Calcium and Mg concentrations generally remain steady within CWD during decomposition.

The increase in N and P concentrations during decomposition is primarily due to immobilisation. Nitrogen concentration may increase in a CWD-piece without any importation due to fungi sequestering the N into their mass, and therefore retaining the N whilst the CWD-matrix is slowly decreased in mass (Bütler *et al.* 2007). However, it is also indicative of sequestration from external sources (Barber and Van Lear 1984). This is a result of translocation from the surrounding environment, and from the fixation of atmospheric N on the surface of, and within, the CWD. Sapwood generally has a higher N and P content than heartwood, and a resulting lower C:N and lignin:N ratio (Idol *et al.* 2001). Barber and Van Lear (1984) found that after clearfelling, the N and P of logging slash was not released to the forest environment until after the regeneration of the forest; except for an initial brief period of minor leaching. This is obviously due to the extended time required for CWD decay. Arthur *et al.* (1993), in a study of a regenerating northern mixed-angiosperm forest 23 yr after clearfelling, found that net

loss of nutrients to the surrounding environment from the CWD took place sometime after a period of decay lasting 23 yr. Foster and Lang (1982), Means *et al.* (1992), and Bütler *et al.* (2007) found that the N:P ratio converged toward 20:1 as CWD approached complete decay. O'Connell *et al.* (1979) and O'Connell and Grove (1987) found that N_2-fixation was higher in the fine-litter of wet eucalypt forests compared to dry eucalypt forests; it is reasonable to assume that this pattern would also exist in relation to N_2-fixation in CWD.

The turnover of the decomposer microbial organisms may also play an important part in the release of CWD nutrients, as the nutrients released by dead micro-organisms may stimulate further colonisation by other micro-organisms, resulting in the net mineralisation of CWD nutrients (Moorhead *et al.* 1996). This would increase the decomposition rate of CWD dependent on successional micro-organism decomposition, and may explain some of the observed time-lag in initial CWD decomposition.

Cosenza *et al.* (1970) suggest that a mutually-beneficial, but not symbiotic, relationship exists between bacteria and fungi, with each group producing compounds that are nutrients for the other. Knutson (1973) and Aho *et al.* (1974) postulated that CWD-decaying fungi utilise bacteria as a nitrogen-source. Indeed, Spano *et al.* (1982) found that fungi decomposed CWD faster when N_2-fixing heterotrophic bacteria were present. Jurgensen *et al.* (1980, 1984) found that heterotrophic bacterial N_2-fixation was not dependent on carbohydrate concentration; they actually found an inverse relationship between N_2-fixation rate and CWD carbohydrate concentration. However, Cosenza *et al.* (1970), Jurgensen *et al.* (1989) and Li *et al.* (1992) suggested that fungi-produced carbohydrates are still utilised by N_2-fixing bacteria, with white-rot fungi producing greater quantities of carbohydrates than brown-rot fungi. This suggests that the heterotrophic N_2-fixing bacteria are also dependent on other nutrient sources as well as the carbohydrates available in the wood. However, heterotrophic N_2-fixing bacteria are unable to utilise cellulose, hemicellulose, and lignin, and rely on other organisms to degrade these substrates to simpler compounds suitable for absorption (Jurgensen *et al.* 1987). This may be a case of the fungi inadvertently 'farming' the N_2-fixing bacteria; providing simple molecules suitable for bacterial growth, then killing the bacteria to obtain the N-compounds manufactured from the fixed N_2. Indeed, Barron (1988) found some species of fungi predate upon living bacteria.

As decay progresses, the fungi experience restricted growth due to the diminished labile content of the wood (switching the fungi from N-limited to being limited by other

nutrient-compounds), with a resulting reduction in predation rate on the N_2-fixing bacteria. This reduced predation rate, due to reduced growth-rate of the fungi, would allow the N_2-fixing bacteria to increase in population size, with a corresponding increase in N_2-fixation rate. Despite fungi growth-rate being limited as decay proceeds, the fungi would continue to provide some simpler-compounds that the bacteria can utilise for growth. It is also possible, that reduced predation, by the fungi, on other bacteria may favour the breakdown of complex compounds by these other bacteria, resulting in a continued supply of simpler-compounds for the N_2-fixing bacteria. However, this reduced availability of simpler compounds for bacterial growth, due to the reduced growth-rate of fungi, may explain the reduced N-concentration found in the latter stages of decay by some researchers (e.g. Grier 1978). Jurgensen *et al.* (1989) found that the white-rotted angiosperms studied, which decayed faster than the brown-rotted conifers, had higher N_2-fixation rates by the resident heterotrophic N_2-fixing bacteria; compared to the conifer wood.

One possible cause of error in determining increase in nutrients is the use of concentrations. It is possible for the concentration of a particular nutrient to increase without a net increase in the amount of the nutrient. This situation would result if the nutrient of interest were removed from the CWD at a slower rate than the C. The use of concentrations must be kept in perspective, as a particular nutrient may actually undergo a net release to the environment, but show an increasing concentration due to a slower-than-carbon release rate. Another cause for error, in interpretation of CWD nutrient concentrations, is the chemical analysis includes intra-cellular compounds of the decomposer micro-organisms, as well as the nutrient-compounds available in the CWD matrix.

Nitrates produced by mineralisation are readily leached from soils (Adams and Attiwill 1984), therefore, any mechanism for regulating the release of N to a slow constant release that can readily be absorbed by plants will benefit the forest environment. CWD is the primary mechanism for storing N and P and releasing it slowly into the ecosystem, preventing excessive leaching to depths inaccessible to tree roots. While the heterotrophic N_2-fixing bacteria found in CWD provide a small proportion of ecosystem N-input, the longevity and the often large quantities of CWD found in ecosystems can account for an accumulation of considerable amounts of fixed N_2 (Jurgensen *et al.* 1984; Li *et al.* 1992), which in turn can account for a substantial proportion of the ecosystem N (Jurgensen *et al.* 1987).

The galleries made by burrowing insects may also increase the leaching rate of nutrients from CWD, especially in wet environments; increased nutrient leaching could result from nutrient-rich water draining out of the CWD to the surrounding environment. The effect of burrowing-insect galleries may increase decomposition by increasing the decomposer organism inoculation rate of the inner wood and by increasing aeration of the inner CWD, but may decrease the decomposition rate by allowing excessive moisture evaporation and nutrient leaching.

A greater understanding of the contribution of CWD to ecosystem nutrient-cycling is needed (Bütler *et al.* 2007). Managed forests lose greater amounts of N to the atmosphere and to aquatic ecosystems (Vitousek and Matson 1984). Management practices that incorporate fuel-reduction-burning exacerbate N-losses from ecosystems, due to the volatisation of N-compounds from the heat of the fire (Attiwill *et al.* 1996), and repeated burning exacerbates this N-loss from ecosystems (Hamilton *et al.* 1991). (Unlike many of the nutrients that are transferred to the soil in the ash from burning, the nitrogenous compounds are lost to the atmosphere.) Whilst *Acacia* growing in the understorey of post-fire regenerating eucalypt-forests have the ability to sequester fixed-N (Ashton 1976), through its symbiotic relationship with the N_2-fixing bacterium *Rhizobium*, it takes in the order of 20 years or more of fire-free growth for the *Acacia* to balance-out the N lost in a typical fire in wet eucalypt forest (Attiwill *et al.* 1996). Generally, the *Acacia-Rhizobium* N_2-fixation increases for up to 80 yr after disturbance, but then decreases thereafter (Attiwill *et al.* 1996), as the *Acacia* are relatively short-lived compared to the eucalypts and decline over time (Lindenmayer *et al.* 2000), and the remaining stored-N is released relatively-quickly as the *Acacia* decompose faster than the eucalypts (Attiwill *et al.* 1996). (It must be stressed, that this pattern of short-term *Acacia* increase followed by long-term decline is a generalisation, and there are exceptions to this pattern.) While it is normal for old-growth wet eucalypt forests to have experienced several non-stand-replacing fires (of low to medium intensity) during their existence, which entail removal of the understorey whilst maintaining the dominant eucalypt-overstorey, resulting in a re-establishment of the shorter-lived *Acacia* in the understorey (Lindenmayer *et al.* 2000), any period of short-interval-fires will cause a reduction in ecosystem N-loading. (Unnatural short-interval fires are predominantly the result of anthropogenic action, such as prescribed fuel-reduction burning, or malicious action by arsonists.) However, if fire is kept out of the wet eucalypt forests for a long time (e.g. 200 yr), and *Acacia* are not able to re-establish in the understorey, then ecosystem N may also diminish. In these situations of reduced or

increased fire-occurrence, CWD may be an important and necessary source of N in the wet eucalypt forests, despite their efficient N-cycling.

Since CWD has its highest nutrient concentration in the highly decomposed state (Fahey 1983), there is no benefit gained by allowing wood to decompose slightly in the field before removing it (for firewood etc.). It must be allowed to decompose completely in the environment if the nutrients are to be cycled back into the ecosystem.

2.2 REVIEW OF METHODS

This component of the literature review concentrates on the different methods used in assessing CWD in the field, assaying samples in the laboratory, and appraising the different decomposition-models used to describe CWD decay. This review covers size requirements in sample-selection, the different surveying and sampling strategies, decay-classification systems, appraisal of the different decomposition-models used in describing CWD-decomposition, and the different laboratory-methods employed to measure sample volume, mass, and density.

2.2.1 SIZE LIMITS OF CWD

Coarse woody debris requires a minimum diameter threshold to distinguish it from fine woody debris and litter (Woldendorp *et al.* 2002b). The range of minimum diameters used to distinguish CWD from fine woody debris and litter varies from 1 cm (Edmonds *et al.* 1986; Turnbull and Madden 1986; Polglase and Attiwill 1992) to 25 cm (Spano *et al.* 1982; Bingham and Sawyer 1988; Currie and Nadelhoffer 2002), and even 30 cm (Brown *et al.* 1998). The 10 cm minimum-diameter threshold has been used by many investigators (e.g. Foster and Lang 1982; Graham and Cromack 1982; Spies and Cline 1988; Spies *et al.* 1988; Delaney *et al.* 1998; Lindenmayer *et al.* 1999; Mackensen and Bauhus 1999; Spetich *et al.* 1999; Chambers *et al.* 2000; Rose 2000; Idol *et al.* 2001; Clark *et al.* 2002; Currie and Nadelhoffer 2002; Woldendorp *et al.* 2002b; Stokland and Sippola 2004; Eaton and Lawrence 2006; Bütler *et al.* 2007); of course, this list is not exhaustive. A survey of the literature showed the most common minimum diameter used is 10 cm, with over 40% of literature read (18 of 44 papers) using this minimum diameter. The second most common minimum size-threshold used is 15 cm, accounting for less than 10% of the literature surveyed (4 of 44 papers). A 7.5 cm minimum-diameter has often been used in forest fuel inventories (Harmon and Sexton 1996; Woldendorp *et al.* 2002a), and this has been adopted by some researchers (e.g. Triska and Cromack 1980; Barber and Van Lear 1984; Grove 2001; Stevenson *et*

al. 2006); slight deviations of this value have occasionally been used such as 7.6 cm (e.g. Jurgensen *et al.* 1984; Sturtevant *et al.* 1997) and 7.61 cm (e.g. Uhl and Kauffman 1990).

The length of the CWD to be sampled must also be considered, as decomposer organisms will colonise CWD from the ends as well as the surface (Leach *et al.* 1937; Harmon and Sexton 1996). Laiho and Prescott (1999) found faster colonisation by decomposer organisms from the ends of wood than in the central-region. A common strategy employed is to take samples at least 50 cm from the end of a log; this requires the CWD piece to be at least 1 m in length.

2.2.2 IN SITU VS. LABORATORY STUDIES

Coarse woody debris decomposing in an artificial environment might produce anomalous results due to experimental manipulation (Daubenmire and Prusso 1963). Laboratory based experiments, where only a few parameters, often only one, are manipulated at any given time, run the risk of ignoring interactions that occur in the natural environment, especially synergistic interactions. Laboratory based decomposition experiments will tend to over-simplify the decomposition process. Therefore, it is recommended that CWD decomposition be determined from samples collected in natural environments.

2.2.3 DECAY CLASSES

Many studies of CWD have used decay-class classification systems. Individual decay classes represent temporal periods in the progression of the decay process for CWD (Temnuhin 1996). If volume or mass of CWD is to be determined for a given area, then each piece encountered needs to be assessed for decay class classification (Woldendorp *et al.* 2002a, b). There has been a great variety of parameters used to distinguish between the different decay classes, with the more elaborate systems, with a greater number of classes, requiring more parameters and/or more subclasses. Decay classes represent a suite of characteristics that change over time, typically including wood density (sometimes referred to as 'soundness'), distortion of typical tree shape (deviation from roundness), and characteristics of the CWD surface substrate. Additional indicative parameters used to determine the stage of CWD decay include coverage by bryophytes, ferns, and phorbs, and the presence and integrity of bark coverage (Arthur and Fahey 1990; Stewart and Burrows 1994; Meggs 1996; Lindenmayer *et al.* 1999; Pyle and Brown 1999). Presence of ants and termites

(Harmon *et al.* 1987) and evidence of insect attack (Stewart and Burrows 1994) have also been used to determine decay class. The presence of saproxylic insects at certain stages of decay have been studied, but this is more for using the decay stage to predict the presence of certain beetles (Grove and Bashford 2003). The presence of basidiocarps (fruiting body of the fungal division Basidiomycota) has also been suggested (Bader *et al.* 1995), although the presence of basidiocarps is not generally recommended, as the applicability of this method may be influenced by seasonality of fruiting. The presence, and integrity, of sapwood has also been used, as well as the presence and extent of heartwood cracking (e.g., Chee 1999; Woldendorp 2000).

Several decay class systems have been used, with most studies adopting a 3-, 4-, or 5-class system (Harmon *et al.* 1986). However, the range of classes used varies from two (e.g., Fahey 1983; McKenzie *et al.* 2000) to eight (McCullough 1948; Söderström 1988). In the literature read, the 5-class systems are the most common, accounting for 57% (27 of 47 papers) of the systems used, with the 2-, 3- and 4-class systems accounting for another 38% (18 of 47 papers) of the systems used. The two-class system assigns CWD into 'sound' or 'rotten' classes, where 'sound' wood is solid, and cannot be easily deformed by kicking with a boot, with the 'rotten' class being easily deformed. The two-class system does not give any indication of CWD age, other than younger or older. The more elaborate decay class systems, however, do afford a measure of CWD age, with the more decayed wood being assumed to have been of the forest floor longer. Due to the variability of initial density of eucalypt CWD, the applicability of decay class systems with more than five or six classes is questionable.

In most forest studies of CWD decay, the intermediate decay classes contain the majority of the CWD (Graham and Cromack 1982; Sollins 1982; Harmon *et al.* 1986; Bingham and Sawyer 1988; Delaney *et al.* 1998; Spetich *et al.* 1999). This pattern is essentially an artefact of the classification system used. Occasionally, this may be the result of a pulse of higher CWD recruitment in the past due to irregular disturbance events (Franklin *et al.* 1987; Pyle and Brown 1999; Spetich *et al.* 1999; Currie and Nadelhoffer 2002), but this would result in an even distribution, across a region, of decay classes with higher CWD loads. However, as this pattern has not been reported on a regional scale, it is assumed that pulsed CWD recruitment is irregular and not the cause of the general trend of higher amounts of CWD in the intermediate decay classes. Rice *et al.* (2004) suggested that ENSO would affect forest ecosystems, although different ecosystems would be affected differently, and Clark *et al.* (2002) found some

evidence suggesting that El Niño/La Niña affects tree-mortality in tropical central-American rainforests. However, the differential pattern of the timing when stress-killed SDTs fall to the ground make it difficult to determine the regional climatic-effect upon stocks of fallen timber. Decay occurring in living trees may also contribute some CWD-wood that is in an intermediate decay-stage when falling to the ground (Franklin *et al.* 1987; Pyle and Brown 1999; Chambers *et al.* 2000).

The most likely cause of the intermediate decay class having the greater amount of CWD is that most of the trees die, and remain standing as SDTs (standing dead trees). Their structural integrity is resilient enough to prevent the SDT from collapsing to the ground until it has reached the intermediate stage of decay (Spies and Cline 1988; Morrison and Raphael 1993; Delaney *et al.* 1998; Laiho and Prescott 1999). (Due to time constraints, a literature-based analysis of this hypothesis was not conducted.) Consequently, a large portion of the dead trees (SDTs) are excluded from the early decay stages. Once the tree has fallen, at an intermediate decay stage, it then decays further before progressing to the following decay stages. This decay ensures that there is less wood, as CWD, in the subsequent latter decay stages than there is in the intermediate decay stage. This pattern would be most evident in areas where natural tree death due to old age, fire, insect attack, and disease kills more trees than wind, flash flood, soil slippage, avalanches, and anthropogenic thinning and harvesting. Decay-state heterogeneity of recruited CWD is also affected by mode of death; Morrison and Raphael (1993) found that SDTs from fire-killed trees fell sooner than the SDTs of trees not killed by fire.

The analyses requirements of the collected data may also predetermine the number of decay classes used for a particular study (Woldendorp 2000); this will also be a function of the variability of the parameters being used to determine the stage of decay (e.g. wood density).

2.2.4 CHRONOSEQUENCE AND REPEATED-MEASURES STUDIES

Due to the longevity of CWD (Franklin *et al.* 1987), the accurate determination of decomposition rates has been problematic (Sinsabaugh *et al.* 1992; Harmon *et al.* 2000), as it has been necessary to study the decomposition process for an extended period of time (Erickson *et al.* 1985; Harmon *et al.* 1986). Some investigators have attempted to study CWD decomposition using time-series experiments (e.g. Edmonds and Eglitis 1989; Alban and Pastor 1993; Harmon *et al.* 1994; Brown *et al.* 1996). With time-series experiments, it is preferable to study decomposition over several years, as there is

year-to-year variation (Witkamp and Van der Drift 1961) and within year (seasonal) variation (Frankland *et al.* 1963). Due to the greater time required to study CWD decay, there has been little interest shown in decomposition dynamics of CWD, relative to the great interest shown in the decomposition of fine litter (Harmon *et al.* 1986; Mackensen and Bauhus 1999).

The majority of CWD decomposition studies have used the chronosequence method (Harmon *et al.* 2000). Studies that have used the chronosequence method include Christensen (1977), Grier (1978), Lambert *et al.* (1980), MacMillan (1981), Foster and Lang (1982), Graham and Cromack (1982), Silvester *et al.* (1982), Fahey (1983), Means *et al.* (1985, 1992), Turner (1986), Harmon *et al.* (1987, 2000), Sollins *et al.* (1987), MacMillan (1988), Saldarriaga *et al.* (1988), Spies *et al.* (1988), Johnson and Greene (1991), Busse (1994), Krankina and Harmon (1995), Frangi *et al.* (1997), Sturtevant *et al.* (1997), Brown *et al.* (1998), Chee (1999), Mackensen and Bauhus (1999), Næsset (1999a, b), Spetich *et al.* (1999), Chambers *et al.* (2000), Harmon *et al.* (2000), Idol *et al.* (2001), Ringvall *et al.* (2001), Preston *et al.* (2002), Ganjegunte *et al.* (2004), Brais *et al.* (2005), Eaton and Lawrence (2006), and Garrett *et al.* (2007); although Harmon *et al.* (2000) and Ringvall *et al.* (2001) used a combination of the chronosequence method and repeated-measures sampling. The chronosequence method involves sampling CWD of different ages, and hence different decay stages, once only (Woods and Raison 1982; Harmon *et al.* 2000). The major benefit of chronosequence sampling is that a study can be made in a relatively short time-period, as opposed to the decades that it would take to follow decomposition of samples with a repeated-measures study. Another benefit of the chronosequence method is there is no sampling of CWD that has been disturbed through prior sampling events (Woods and Raison 1982); this eliminates any bias that may occur from repeated-measures sampling. Chronosequence sampling also allows completely random sampling, which is a problem with the repeated-measures method of sampling; subsequent sampling events are not random. "Classical statistical methods" assume that observations are independent (Millard and Neerchal 2001). Schowalter (1992) and Schowalter *et al.* (1998) used a repeated-measures study, but avoided sampling-independence problems by sampling different logs at different times; different sample-logs were allocated for sampling at different times (they performed a placement-experiment where sound (nil-rot) logs were cut from living trees and placed on the forest floor in close proximity to each other). However, the chronosequence method does have drawbacks, such as the lack of knowledge of the original condition of the CWD (did it fall at death, or did it exist as an SDT before falling) and the original

volume and wood-density (Means *et al.* 1985; Harmon *et al.* 2000). The problem of unknown initial CWD volume is discussed in section 2.2.5.7 (*Constraints of Models*; *VOLUME REDUCTION DURING DECOMPOSITION*). Chronosequence sampling also has larger variances in wood density than would be encountered if samples were continually taken from the same pieces of CWD. Microclimate differences between sites also increase the variability of the data collected, as these differences can lead to different decay rates (Harmon *et al.* 2000).

A further problem with the chronosequence method is obtaining accurate sample-ages (Næsset 1999a), especially when using indirect methods, such as dendrochronology, to age samples (Daniels *et al.* 1997). (There can even be differences in the same log — this point is discussed in section 2.1.1.3 *Controlling Factors of Decomposition*; *SUPPORTING MATRIX QUALITY*.) When using forest inventory data, the chronosequence method is also exposed to the quality of data collected in the past. It has been noticed that many trees have been missed at a particular survey time, only to be measured during the next survey. When using forest inventory data, tree-fall is usually calculated as the median date between the last recorded date and the subsequent survey date. A problem can arise if a tree was recorded at a specific date, and was missed at the subsequent date, despite being alive and standing, and was found to have fallen at the next survey date. The tree-fall date would be calculated as the median date between the first and second survey dates, when it should be recorded as the median date between the second and third survey dates. Depending on the time between inventory survey-dates, considerable variability in CWD age estimations can occur.

2.2.4.1 Decomposition Vector Method

Harmon *et al.* (2000) developed a hybrid method of assessing CWD decay where they combined the chronosequence method with the repeated-measures method; they called this the "decomposition-vector method". The reasoning behind this approach was that the chronosequence provides samples from varying stages of decomposition, whilst the time-series re-sampling provides measures (or "vectors"; Harmon *et al.* 2000) of change against time. Harmon *et al.* (2000) performed an initial chronosequence survey in the St. Petersburg and Novgorod regions of NW Russia, and then re-sampled the same sites three years later. However, they found no significant differences using this method compared to the results of a once-only sampling. Despite the decomposition-vector method failing to show significant differences against the chronosequence method, over the three-year period of the Harmon *et al.* (2000) study, it

may prove an effective method for longer studies, although justification for an extended period of sampling may be difficult. (The study of Harmon *et al.* (2000) was conducted in NW Russia, which has a mean annual air temperature of 4°C and mean annual rainfall of 600-800 mm.) This method may be viable for studying the CWD of forests in the wet tropics where environmental conditions are most conducive to faster decay rates. The wet tropics, at any rate, will most likely be the best environment to determine the potential worth of this method.

2.2.5 DECAY MODELS

Rate of litter decomposition in a forest ecosystem has a strong influence on ecosystem productivity (Woods and Raison 1982). Due to heterogeneity of site factors, e.g., microclimate and decomposer organism availability, within a forest, spatial variability in decay rates occur (Boddy and Swift 1984). The litter decomposition rate also influences the release rate of carbon (C), which was sequestered in the growing plant, back to the environment (IPCC 1996, 1997b).

Mathematical models of biological systems are used for an assortment of reasons, including the decomposition of CWD and other litter components (Moorhead *et al.* 1996). Ecology and environmental management rely heavily upon the output of models that describe biological processes and ecosystem functioning (Anon 1983; Moorhead *et al.* 1996). Individual models operate at a specific resolution (scale), dependent on their predetermined use and the individual variables included (Karjalainen 1996). Many models can be included in a larger model that operates at a higher level in a hierarchical structure. That is, several models that describe specific functions within an ecosystem can be included in a larger model, which is used to describe ecosystem functioning. Oreskes *et al.* (1994) criticised the use of models for predictive purposes. However, while individual experiments ultimately provide the information environmental management decisions are based on, models are required to predict future ecosystem responses (Karjalainen 1996). The use of extrapolation in models is necessary to predict likely ecosystem response to differing scenarios, which is required if environmental managers are to be prepared in advance. It is better for managers to be proactive, rather than reactive; 'to be forewarned is to be forearmed'.

The decomposition process can be modelled by fitting a mathematical model, to the data, which estimates parameter values describing change over time (Wieder and Lang 1982).

2.2.5.1 Linear Model

Linear models are conceptually the simplest models used to describe the decomposition of CWD. They are of the form:

$$\frac{Q_t}{Q_0} = 1 - k.t \qquad \textbf{Equation 2-1}$$

Where: Q_t = amount remaining (density, volume etc.),

Q_0 = original amount (density, volume, etc.),

k = decay model constant, and

t = length of time CWD has been on the ground.

While easy to use, the linear model does not account for the decreasing instantaneous rate-of-decay of CWD decay, due to proportional changes in the individual component decay rates over time. The linear model is inappropriate for the decomposition of litter consisting of separate compounds, each with a different decay rate (Wieder and Lang 1982); although it is still commonly used.

2.2.5.2 Input:Biomass Ratio Model

Input:biomass ratio models rely upon knowing the mass of the standing litter per unit area, and the litter input per unit area over a given time period. Assuming the rate of decomposition to be constant, the decay rate can be deduced from calculating the difference from the litterfall mass and the litter accumulation mass. The difference between the input (litterfall mass) and the increase (accumulation mass) is assumed to be due to decomposition (Jenny *et al.* 1949; Olson 1963). A decomposition rate slower than the litter input rate results in an accumulation of litter over time (Spain 1984).

While conceptually simple to use, these models do not lend themselves to analysis of litter in different stages of decay, and to the calculation of the residence time of each decay stage, which is a common requirement of CWD decay studies. Additionally, the length of time for CWD to pass through the decomposition process, along with episodic inputs, would require input:biomass-model studies to be conducted over decades for CWD. Input:biomass models are, therefore, more suited for fine litter decomposition than CWD decomposition.

2.2.5.3 Single-Exponential Model

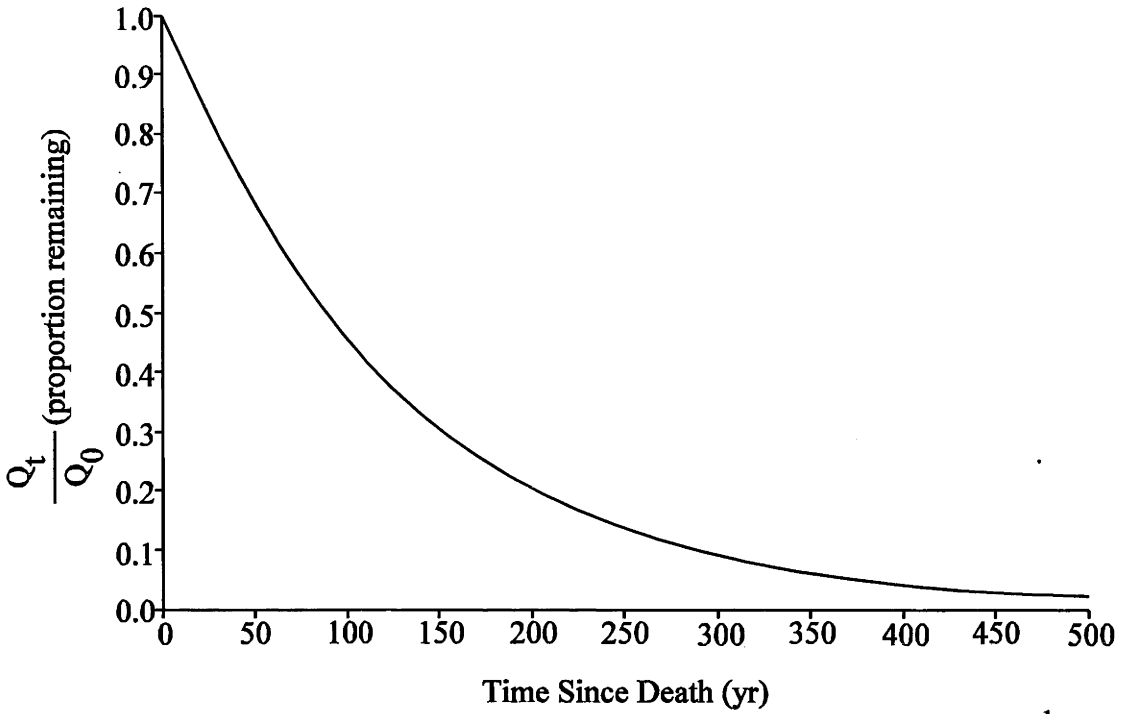


Figure 2-3. Curve of the Single-exponential model, with a *k*-value of 0.008 yr^{-1}.

The most common model used to describe CWD decomposition is the single exponential model (Wieder and Lang 1982), and has been used to estimate CWD decay rates in various ecosystems throughout the world (Means *et al.* 1985). The model uses a single constant (*k*-value) to characterise proportional loss over time, making it an appealing model (Wieder and Lang 1982) due to its ease of use and simplicity in interpretation. Jenny *et al.* (1949) were the first to use the single-exponential model (SEM) to describe litter decomposition. The use of this model was further advanced by Olson (1963).

$$\frac{Q_t}{Q_0} = e^{-k.t} \qquad \textbf{Equation 2-2}$$

Where: Q_t = amount remaining at time t (density, volume, mass),

Q_0 = original amount (density, volume, mass),

k = decay model constant, and

t = length of time CWD has been on the ground.

2.2.5.4 Double-Exponential Model

Idol *et al.* (2001) found significant differences in the chemical concentrations of sapwood and heartwood in the intermediate decay classes of oak and hickory CWD, which they suggest may lead to different decay rates of the sapwood and heartwood. Mackensen and Bauhus (1999, 2003) suggested that a dual-component exponential model might be more appropriate for eucalypts, to account for differences in decay resistance between sapwood and heartwood.

Wieder and Lang (1982) assumed that CWD is composed of two distinct fractions, the easily decomposed labile-fraction, and the decay resistant recalcitrant-fraction, which provided the rationalisation for expansion of the single-exponential model to account for the two different fractions. This model is known as the 'double-exponential model' (DEM).

$$\frac{Q_t}{Q_0} = W.e^{-k_1.t} + (1-W)e^{-k_2.t} \qquad \textbf{Equation 2-3}$$

Where: Q_t = amount remaining at time t (density, volume, mass),

Q_0 = original amount (density, volume, mass),

W = proportion of initial CWD as labile fraction (labile fraction proportional weighting)

k_1 = decay model constant for labile fraction, and

k_2 = decay model constant for recalcitrant fraction, and

t = length of time CWD has been on the ground.

The ratio of 'W' and '(1-W)' is the initial (time = 0) labile-fraction:recalcitrant-fraction ratio. The DEM treats the two fractions as mutually exclusive, and does not consider the movement of material between the recalcitrant and labile pools during the decomposition process (Wieder and Lang 1982).

Due to the DEM relying on the labile fraction to give the k_1-value, it is imperative that young CWD wood with the labile fraction is included in the analyses. If samples including the labile fraction are not collected, then k_1 cannot be calculated (which means that the double-exponential model is inappropriate to the analyses of the particular sample set). If a particular CWD piece has an initial labile fraction

accounting for, say, 20% of the total wood volume, with a decay constant of $k_1 = 0.1$ yr^{-1}, and the decay constant of the recalcitrant fraction is $k_2 = 0.0075$ yr^{-1}, then after 30 yr of decomposition, the labile component would account for less than 1.6% of the remaining wood (see Figure 2-4). The overall decay curve would then be driven by the decay rate of the remaining 98.4% of the wood (the recalcitrant fraction with decay rate of 0.0075 yr^{-1}). (As Heartwood forms the greater proportion of the wood in eucalypt forests (Mackensen and Bauhus 1999), an arbitrary value of 80% recalcitrant-fraction (20% labile-fraction) was used in this example.)

The recalcitrant-fraction will dominate the decay curve due to its greater initial proportion and longevity (Minderman 1968). The slower the recalcitrant-fraction decays, or the larger the initial proportion it occupies, the greater the influence it has on the decay curve.

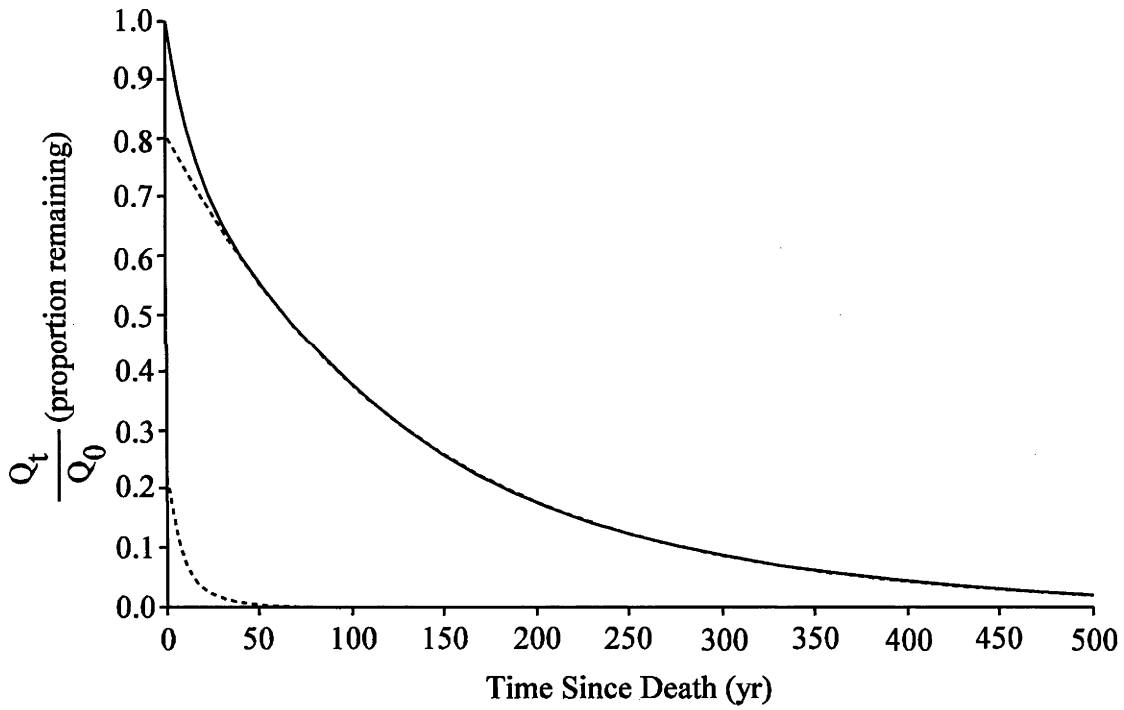


Figure 2-4. Double-exponential model graph, showing the labile fraction and recalcitrant fraction (- - -; upper line is the recalcitrant fraction), and the overall DEM decay curve (———).

Another problem with the double-exponential model, is that CWD age (time since death) must be extremely accurate for the 'younger' samples, as any slight error in estimating age will cause a much greater error in calculating k_1 than it will for calculating k_2. This leads to a requirement that young CWD samples must be included in the analysis, or the decay curve will only be influenced by the decomposition rate of the recalcitrant-fraction (as the labile-fraction has already decomposed).

2.2.5.5 Sigmoidal Decomposition Model

Harmon *et al.* (2000) suggested three discrete sequential phases occurring in CWD decomposition: (i) an initial period of slow decomposition during the period of colonisation by decomposer organisms, (ii) a subsequent period of fast proportional loss as labile compounds are degraded, and (iii) a final period of slowing proportional loss as recalcitrant compounds are degraded. A sigmoid model could be used to describe such a pattern of decomposition.

$$\frac{Q_t}{Q_0} = 1 - \frac{1}{1 + H.e^{-k_s.t}}$$ **Equation 2-4**

Where: Q_t = amount remaining at time t (density, volume, mass),

Q_0 = original amount (density, volume, mass),

H = horizontal (time) shift due to period of decomposer organism colonisation (phase 1 of CWD decomposition),

k_s = sigmoid decay model constant, and

t = length of time CWD has been on the ground.

Laiho and Prescott (1999) found a sigmoidal-pattern in mass-loss of *Pinus contorta* Douglas (a conifer) logs they studied. Næsset (1999b) found there was a delay to the decomposition of the *P. abies* (conifer) logs studied, and suggested that this was due to a colonisation period, whilst Harmon *et al.* (1987) found that it took several years for the decomposer organisms to reach the centre of larger-diameter logs in a mixed-conifer forest. Bütler *et al.* (2007) found an increase in *P. abies* wood-density, from green-density, to decay-class-I samples, with a decrease in density in subsequent decay-classes. Means *et al.* (1985) suggested that it might be common for decades to pass before colonising decomposer organisms to reach the centre of larger logs. (Initial wood-density would influence the speed that decomposer organisms are able to traverse to the interior of logs; with denser-logs providing greater resistance to inward infection.) Whilst there is undoubtedly a colonisation period by many decay organisms, many of the decomposer organisms are already present in the wood of the tree when it is alive, and these continue to degrade the wood when the tree passes to the CWD pool (Hopkins *et al.* 2005). This may make detection of the colonisation phase difficult in some CWD.

It is interesting to note that Hicks *et al.* (2003) found a sigmoidal-pattern to CWD N_2-fixation, over time; they suggest that this is a reflection of the colonisation-pattern by heterotrophic N_2-fixing bacteria. Since N is an important growth-requiring nutrient

in the N-poor CWD (see section 2.1.4.1 *Nitrogen* for a discussion of this point), it is possible that CWD-decomposition may follow this N_2-fixation pattern closely where available N-concentration is the most limiting factor to decomposition.

2.2.5.6 Asymptotic Model

Asymptotic models (see Figure 2-5) can be used to describe CWD decomposition where the recalcitrant material appears to be totally resistant to decay (Wieder and Lang 1982). This model only applies to models using wood density as a means of modelling CWD decay, as the mean density increases until it reaches the density of the most-recalcitrant fraction of the wood, where it remains stable thereafter. Volume and mass measurements are unsuitable for use with the asymptotic model, as measurements decrease (instead of increasing) until the remaining volume or mass consisted of the most-recalcitrant fraction, and would remain stable thereafter. As all plant molecules are susceptible to degradation from decomposer organisms, the validity of asymptotic models to describe CWD decomposition is questionable (Wieder and Lang 1982).

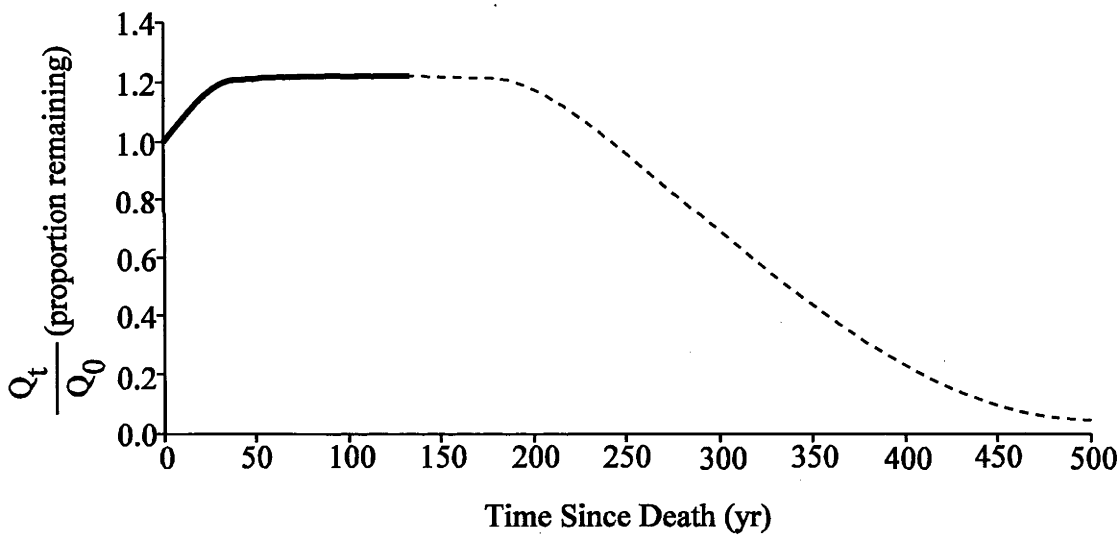


Figure 2-5. Asymptotic model (———) forming portion of exponential-growth-and-decay curve (- - - - -). This shows how incomplete CWD age data can make an exponential-growth-and-decay curve appear to be asymptotic.

The appearance of decay-exempt CWD is likely to be the result of the affects of (i) wood chemistry, both nutrients and toxins, (ii) efficiency of the decomposer organisms present, (iii) the ability of the decomposer organisms to colonise the CWD piece, and (iv) the prevailing microclimate of the CWD substrate (moisture, temperature, and fire régime). The additive affects, and interactions, of these factors may slow decomposition to such an extent that they seem to be exempt from decay, but they will

eventually decay, even though it may take centuries, especially in conditions of unfavourable microclimate.

2.2.5.7 Constraints of Models

VOLUME REDUCTION DURING DECOMPOSITION

CWD density reduces during the decomposition process (Lambert *et al.* 1980; Alban and Pastor 1993; Arthur *et al.* 1993; Delaney *et al.* 1998; Currie and Nadelhoffer 2002), which has led to many investigators using density loss to determine the decay rate of CWD. However, if the CWD piece compresses (collapses inward) during decomposition, then the density will be higher than it would be if compression did not occur. This gives the impression that less mass has been lost than has actually occurred. Consequently, if collapse occurs, the artificially high density would lead to an underestimation of the decay rate (Fahey 1983).

Allometric equations can be used to convert inventory tree-dimensional-data to tree biomass, via volume calculations (Keith *et al.* 2000); allometry allows the calculation of one variable by the measurement of a covariate (Medhurst *et al.* 1999). The estimation of tree volume and/or mass at time of death, such as by using inventory DBH measurements, will allow the calculation of proportional mass loss due to collapse, and provide a correction factor where density can be used to calculate biomass of CWD (Harmon *et al.* 2000). While generally the preferred method, this correction is not always available, due to incomplete inventory records, difficulty in matching individual CWD pieces with inventory data, and occurrences where trees were not measured prior to harvesting.

Biomass changes incorporate both volume and density changes (Lambert *et al.* 1980), and potentially are the most accurate method to use. However, volume is not always easy to determine, especially in older CWD. Fragmentation results in volume and mass loss, and the fragments are not always easy to find on the forest floor, and accurate searching can take some considerable time, especially for larger CWD pieces. Fragmentation undoubtedly led to the pattern observed by Brown *et al.* (1998), where they found volume-reduction without any decrease in the wood-density. The omitting of fragments can lead to overestimation of the CWD decomposition rate, as greater volume and mass loss is calculated than has actually occurred.

It must be kept in mind when calculating CWD decay rates, that volume and mass methods may overestimate decay rates (due to fragmentary loss), and density methods have the potential to underestimate decay rates (due to compression).

Volume change can also be a source of error when samples are not soaked prior to volume measurement. If the CWD samples are not saturated, shrinkage may artificially reduce the volume of the sample. This error exists for field samples that are not saturated with water, and is further exacerbated for volume measurements taken after drying in an oven. Alternatively, volume may be overestimated if samples are taken from the field, which are saturated, and the excess water is not allowed to drain away before immersion in a water tank to measure water-displacement volume.

The expected *k*-value order (volume method > mass method > density method) was not found by Harmon *et al.* (2000), who found *k*-values in the order mass method > density method > volume method. If the proportional volume-reduction is less than the proportional mass-loss (due to little fragmentation or collapse), then the pattern of Harmon *et al.* (2000) will occur. The observed pattern would be the result of the wood remaining structurally intact, to some extent, during the decomposition period (the samples ranged between 1 and 70 years in age). That is, the wood would have been losing mass, but the structure generally maintained its physical dimensions, resulting in a low-density material with little change in external dimensions. (The volume was "undried or green volume", which suggests that the volume was either measured from physical dimensions, or was measured using water displacement without removing residual water from the sample; (both of which would overestimate the volume of the actual wood).

TIME CONSTRAINTS

In a 16-week study of freshly felled boles, Tainter and McMinn (1999) found that the sapwood density of *Quercus spp.* decreased, but that of *P. taeda* increased, and the heartwood density of both species increased. The increase in heartwood may be due to the mass of the colonising decomposer organisms. During the initial colonisation period, the decomposer organisms would have spent more resources in colonising the heartwood than they have extracted from the heartwood, resulting in an initial increase in heartwood mass. Over time, the density of the heartwood will decrease as resources are translocated away from the heartwood, especially by fungi.

The above shows the problems with short-term studies of CWD decomposition. The changes in density are occurring during the decomposer-organism colonisation phase of the CWD. Density methods of CWD decomposition would be more effective in long-term studies, or with chronosequence studies incorporating older logs as well as younger logs. The incorporation of older CWD was recognised by Erickson *et al.* (1985).

2.2.5.8 *Discussion — Comparison of Models*

The situation where more than one model can describe an observed pattern is known as "nonuniqueness" (Oreskes *et al.* 1994). Where models are non-unique, simplicity, and ease of implementation, may be used to select the most appropriate model. This section reviews the models in this context.

As the simpler molecules are degraded first (Moorhead and Sinsabaugh 2000), there is a rapid initial loss of CWD-mass during decay, but as this relatively labile component decreases, the more recalcitrant components of the CWD account for a larger proportion of the remaining mass. This leads to an ever-slowing instantaneous rate of decay. This affords the CWD an exponential pattern of mass loss during the decay process. Lambert *et al.* (1980) preferred the single-exponential model to the linear model, based on theoretical grounds. Although they did not state the theoretical reasoning for their preference, it is probably because, as decay proceeds, a greater proportion of the remaining wood consists of the slower-decaying recalcitrant material.

Besides using the double-exponential decay model (DEM) to separate the relative contributions of heartwood and sapwood, an equally valid argument could be made for a triple-exponential decay model (TEM). This would be based on the three classes of substrate components of CWD, the extractives, acid insoluble fraction, and acid soluble fraction (Moorhead *et al.* 1996), which are degraded by glucosidases, oxidases, and cellulases, respectively (Moorhead and Sinsabaugh 2000). Indeed, since both the sapwood and heartwood are made up of the same chemical constituents, albeit in different proportions, the argument must follow that it should be the chemical constituents of these components, and their proportions, that should be analysed for their affect on decay rates. Indeed, since bark, sapwood, and heartwood, all decompose at different rates (Maser *et al.* 1988), an argument could be made to analyse the different proportions of chemical constituents in these three wood-structures, with the interaction of the different proportions of the bark, sapwood, and heartwood.

Minderman (1968) suggested that individual plant compounds decay exponentially at different rates, and advocates calculating the decomposition rate for each individual compound, and using the sum of these to calculate an overall decay rate. The problem here, is how many of the chemical constituents of the CWD should be measured for their affect on decay rates? It is obvious that the exponential decay model chosen should have the same number of additive terms as there are parameters being analysed. This may make effective analyses overly complicated, and produce a meaningless model that is almost impossible to apply, especially for comparison to the literature where often very little data is available.

Wieder and Lang (1982) suggested that the DEM is a compromise between the SEM and the recommendations of Minderman (1982). However, the compromise is exactly that, a compromise. The DEM separates many individual decay rates into two groups, which are treated as mutually exclusive, when, in fact, the individual decay rates occur along a continuum.

The double exponential model is also problematic concerning eucalypt decay, as the inner heartwood decays much faster than the outer heartwood. It has been observed in the field (*pers obs.*) that the outer heartwood persists for a relatively long time after the sapwood and inner heartwood has decayed; Scheffer (1957) found the outer heartwood of the conifer *T. plicata* to also be more decay-resistant than the inner heartwood. If the differences in decay rates between sapwood and heartwood are being calculated, then surely, the difference between inner and outer heartwood decomposition should also be measured. In both central Queensland and the Northern Territory (Australia) eucalypt outer heartwood casings have been observed weathering; fragmentation due to loss of structural integrity rather than *in situ* decomposition. Besides the outer heartwood being composed of more recalcitrant material than the inner heartwood, which results in a slower decay rate, the exposure of the outer heartwood to the surrounding environment creates an ever-changing environment for the decomposer organisms, which may further reduce the decomposition process in the outer heartwood. The relatively stable moisture and temperature regime of the inner heartwood may allow a faster decomposition rate due to the microclimate being conducive to the presence of specialist decomposer organisms with specialised enzymes. This is opposed to the probable existence of a greater proportion of generalised decomposer organisms in the outer heartwood, which may have to switch between different enzymes to maintain metabolism at different temperature extremes.

Another problem with the double-exponential model is that it is difficult to use with many statistical packages, whereas the single-exponential model is easy to use. This difficulty makes the double-exponential model unavailable to many investigators, even some of those who may wish to use it. This may be the reason behind Mackensen and Bauhus (1999) stating that the double-exponential model is superior to the single-exponential model for analysing eucalypt decay, yet only analysed their data using the single-exponential model. (Although they did state "it is very easy to fit multiple exponential models to decay data").

It is probably better to use the single exponential decay model to describe decomposition occurring over a long time, as it gives a good general indication of the decay process (Means *et al.* 1985). The application of the single-exponential decay model is especially pertinent to CWD decay, as this is a slow process, often taking centuries to complete.

The argument for usage of the DEM over the SEM is when sapwood and heartwood are very different, in either density or chemical composition. However, when the difference is greater, the greater the curve is dominated by the curve of the recalcitrant fraction, which resembles more of a SEM curve (see Figure 2-4). After the short decay period, where all of the labile material has decayed away, the curve is solely determined by the decay of the recalcitrant material. This situation is even more pronounced in wood where the recalcitrant fraction accounts for a greater proportional amount of the CWD at $t = 0$. The DEM is only of advantage over the SEM when looking at the short-term decay dynamics. If long-term decay dynamics are of interest, the SEM is just as informative as the DEM (see Figure 2-6), and, as Means *et al.* (1985) state, if two models explain the variability equally well, the most parsimonious model should be used (which in this case is the SEM). Additionally, distinguishing between sapwood and heartwood is extremely difficult with many eucalypts, which may limit the applicability of the multiple-exponential models with respect to eucalypt decay studies.

Several other models have been used to describe decay patterns. Quadratic and power models have been used, but are inappropriate for CWD decay; see Wieder and Lang (1982) for a discussion of these models. When modelling decay rates, it is imperative that the initial proportion equals 1, that is, at $t = 0$, $Qt/Qo = 1$ (Wieder and Lang 1982). If the regression does not predict a value of 1 at $t = 0$, then comparison of individual k-values is meaningless (Wieder and Lang 1982). The exponential models are the most realistic biologically (Wieder and Lang 1982).

Another major advantage of the SEM is that direct comparisons using analysis of covariance (ANCOVA) can be made between individual decay curves (Snedecor and Cochran 1980; Sokal and Rohlf 1995; Zar 1996; Underwood 1997).

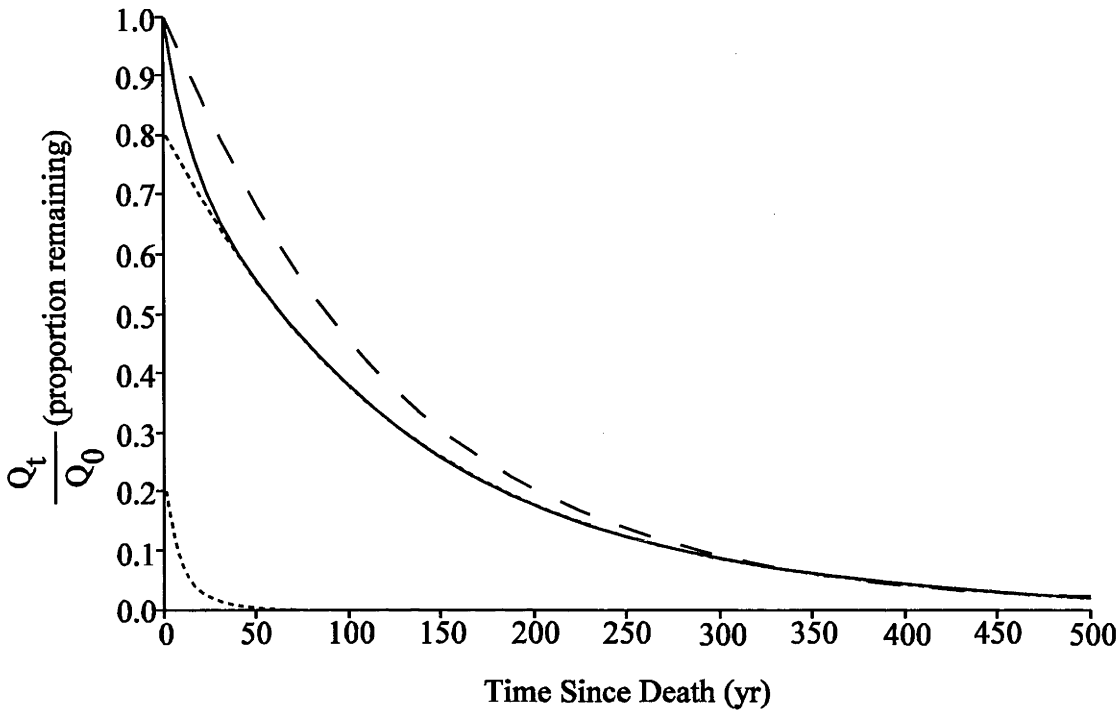


Figure 2-6. Single-exponential model (— — —) and double-exponential model with the labile and the recalcitrant fractions (- - -; upper line is recalcitrant fraction), and the overall DEM decay curve (———) shown. SEM *k*-value = 0.008 yr^{-1}. DEM values are: W = 0.2, k_1 = 0.1 yr^{-1}, and k_2 = 0.0075 yr^{-1}. The values for the SEM and DEM curves have been arbitrarily chosen for clarity of presentation, and do not represent analyses values obtained from a common dataset.

Lambert *et al.* (1980) suggested calculating separate *k*-values for losses due to mineralisation and respiration (k_m) and fragmentation (k_f), with the overall *k*-value being the sum of k_m and k_f. This method is appropriate for determining *k*-values using volume loss or mass loss, but is of no use when using sample-density alone. (Sample-density is the density of the individual samples, g cm^{-3}, and not the field-density, which is the amount of CWD per unit area; e.g., m^3 ha^{-1} or Mg ha^{-1}.) The density-method of calculating the decay model coefficient only provides the *k*-value for the loss due to mineralisation and respiration (Lambert *et al.*'s 1980 k_m-value). However, if the CWD piece fragments, the fragment does not decay immediately (Rice *et al.* 2004), nor does decomposition cease; the CWD piece continues to decay alongside the main piece of CWD. In respect to the density-method, it does not matter whether the piece decays as a separate fragment or if it decays attached to the main bole, as it continues to decay

either way. Therefore, when using density to determine the decay model coefficient, the k-value derived is the actual k-value, and not the k_m-value. In other words, the density-derived k-value incorporates k_m and k_f into a single k-value. One source of error to note, though, is that the components that slough off, due to fragmentation, will have a greater surface-area-to-volume ratio than the remaining bole, and the fragmented component could be expected to decay faster than the major portion remaining. This leads to the k-value being determined from the density decrease of the most resilient component of the original bole, which may lead to underestimations of the overall decay rate (Harmon and Hua 1991), although, it must be said, the fragmentation will also increase the surface-area-to-volume ratio of the remaining bole, potentially increasing its decay rate, albeit to a lesser extent.

For environmental management of CWD, the SEM is undoubtedly the best decomposition model to use, as it gives a good approximation of the decomposition process, and requires much less information than the multiple-exponential models. The large dataset requirements for the effective use of the multiple-exponential models (individual nutrients and toxins, microclimate factors, decomposer organism species composition and inoculation abilities, related to dispersal ability) is really only necessary for the study of the physiology of decaying CWD.

Laiho and Prescott (1999) used two different models to describe decomposition in three different species of conifer. Whilst the models chosen were a 'best-fit' to the three individual species, and therefore technically correct, it makes comparison of decay-dynamics between the three species awkward. Using the SEM, in addition to the chosen models, would have made comparison of the decay-dynamics more meaningful. It must be mentioned that Laiho and Prescott (1999) were primarily concerned with predicting CWD-loadings, and not with comparison of decay rates between species.

Due to the SEM being an 'overall' representation of the decay process, it should be regarded as a representative, albeit imperfect, model of decomposition (Spain 1984).

EMPIRICAL MODELS VS MECHANISTIC MODELS

The inclusion or exclusion of crucial driving variables determines the quality of the predictive ability of a particular model (Moorhead *et al.* 1996). Moorhead and Sinsabaugh (2000) state that there are two types of models used to describe the CWD decay process (i) empirical models which describe the decay process using only time as

the predictor variable, and (ii) mechanistic models that describe the decay process as a function of time and underlying driving-variables of the decay process.

Most decomposition models associate decay rate to substrate quality and site microclimate (Moorhead and Sinsabaugh 2000), but neglect the decomposer species present, and their adaptations to extremes (Whitford *et al.* 1981). The exclusion of some important decay-driving factors in a model, or usage of a model with values outside the ranges of the variables used to create a model, may result in predictions, based on extrapolation, more inaccurate than extrapolation of a simple empirical model. Despite the generally accepted tenet that mechanistic models are accurate during extrapolation, mechanistic models are only accurate for the conditions for which they were developed, and containing the same suite of decomposer species. The acceptance of mechanistic models being accurate during extrapolation is based on the assumption that the decay-driving factors behave in a consistent manner (Moorhead and Sinsabaugh 2000), however, as Whitford *et al.* (1981) found, this assumption must be treated with a measure of caution. Before new environments, or novel situations, are analysed with a mechanistic model, there should be a measure of 'truthing' used to validate the usage of the model. The incorporation of underlying CWD decay-driving processes in mechanistic models, makes them more accurate than empirical models during extrapolation, providing all major driving-factors are incorporated into the mechanistic model.

The requirement for a much greater dataset, incorporating expensive and time-consuming chemical analyses, is a major disadvantage of the mechanistic decay models over the simpler empirical models (Moorhead *et al.* 1996). The added complexity of the mechanistic models may be harder to interpret, due to greater uncertainty of parameter estimates (Moorhead *et al.* 1996). It is imperative that the interactions between factors are also included in the mechanistic model, not just factors acting independently.

Chojnacky and Heath (2002) stated that empirical models should not be extrapolated to other areas for which they were not developed. However, if other areas have similar climatic conditions, and the same suite of species represented, then an argument can be mounted for cautious application of the model.

Despite Moorhead *et al.* (1996) stating that empirical models, such as the SEM, should not be used outside the range of the data used in the construction of the model, it is necessary in an ecological management setting to extrapolate decay curves beyond

the maximum age of the samples collected. Extrapolation is necessary to establish the time required for CWD of different decay stages to form after a CWD-removing event (such as CWD harvesting for fuel wood); as CWD in different stages of decay performs different ecosystem functions. The model would undoubtedly be more accurate with older CWD samples included, but these are not always available, especially if programmed CWD removal has occurred, as this is usually absolute.

2.2.5.9 Calculation of Time for CWD Decomposition

Calculated decay-model constants, of the single-exponential-model, can be used to predict the amount of wood remaining at a given time in the future providing there is not any change in microclimate or other factors affecting the natural decomposition of the CWD (Næsset 1999a).

Jenny *et al.* (1949) and Olson (1963) both calculate the time of CWD decomposition as the time taken for 95% of the original mass to be lost; this is known as $t_{0.95}$. They calculate this as 3/k; which is equivalent to 5% of original mass remaining (95% mass loss). Some investigators to use $t_{0.95}$ are Mackensen and Bauhus (1999), Rose (2000), Mackensen *et al.* (2003).

To calculate the time taken for a certain proportional amount (α) of the wood to decompose, the following formula can be used:

$$t_{\alpha} = -\frac{\ln(1-\alpha)}{k}$$

Equation 2-5

For example, to calculate the time taken for 95% (0.95 proportion) of the wood to be lost due to decomposition, we calculate:

$$t_{0.95} = -\frac{\ln(1-0.95)}{k}$$

If the calculation of time taken for a certain proportional amount remaining (β) is preferred, then the above formula can be modified to:

$$t_{\beta} = -\frac{\ln(\beta)}{k}$$

For example, to calculate the time taken for only 5% (0.05 proportion) of the wood to be remaining, we calculate:

$$t_{0.05} = -\frac{\ln(0.05)}{k}$$

MacMillan (1981) used 90% ($t_{0.90}$) reduction in wood density as the cut-off where the log ceased to be CWD, and had become humus.

2.2.6 FIELD SURVEY METHODS

Variability of carbon sequestration in CWD can be caused by differences in forest age and species composition, as well as heterogeneity in climate and soil nutrient availability and concentrations, and can be affected by differences in site management practices (Anon 1998). Christensen (1977) stated that if you separated a heterogeneous (area with clumping) region into separate homogeneous strata, you will have a resulting gain in precision over simple random sampling. This technique is also recommended by Anon (1998). The stratified sampling technique is considered a valuable tool to obtain greater precision in estimates of amounts of CWD in the environment, which inherently show clumped distributions.

The decomposition rates of leaf litter are relatively easy to calculate due to rapid decay (Boddy and Swift 1984). However, wood usually takes decades to decompose completely (Swift *et al.* 1976; Swift 1977). The distribution of CWD is also variable, both temporally (Christensen 1975; Boddy and Swift 1983) and spatially (Swift *et al.* 1984). Coarse woody debris is recruited at different stages of decay (Boddy and Swift 1983); some trees are knocked over when alive, and others fall after having stood many years after dying. Consequently, the determination of CWD decomposition rates requires different strategies to those used for leaf litter (Boddy and Swift 1984).

Ringvall *et al.* (2001) suggested sampling CWD using two-phase sampling (also known as double sampling) when *a priori* information is not available. They suggested conducting a large sample size in the initial sampling phase, and measuring an auxiliary variable. Then a second phase of sampling is to be performed using a smaller sample size, where the variable of interest is measured directly. This second phase of sampling is to be used to calibrate the auxiliary variable measured during the first phase of sampling. Ringvall *et al.* (2001) initially (first phase) performed a large-sweep of the area counting the number of CWD pieces, and then (second phase) measured the dimensions of the CWD contained within sub-plots of the area covered by the initial sampling-phase. The study by Ringvall *et al.* (2001) was done as an assessment to using relascope-sampling to assess CWD loadings in the forest environment. The authors concluded that the two-phase approach to relascope-sampling of CWD has the potential to be more efficient than single-phase (one-time) sampling.

2.2.6.1 Plot-Based Vs. Line-Intersect Surveys

The volume of CWD in the environment has traditionally been surveyed by either plot-based or line-intersect (line-intercept) sampling. There have been variations in the applications of both methods by investigators (Woldendorp *et al.* 2002a).

PLOT-BASED (AREAL) SURVEYS

Woody biomass has traditionally been measured using allometry (Eamus *et al.* 2000). However, CWD biomass is not easily calculated from DBH for CWD, due to heterogeneity of density as the wood decays. In plot-based ('areal') sampling, the end and central diameters of the log need to be measured, as well as length. Plot-based methods also tend to give inconsistent, if not imprecise, estimates of CWD volumes if the CWD is sparsely distributed (Ringvall and Ståhl 1999a). Boddy and Swift (1984) stated that the size of the plots should be increased in areas where CWD density is low, in order to increase the number of pieces of CWD surveyed, and hence, increase accuracy. Sites with high CWD heterogeneity should also be sampled with larger plot sizes (Woldendorp *et al.* 2002a). This is easily achieved in sampling designs utilising variable radius plots (Harmon and Sexton 1996).

LINE-INTERSECT SURVEYS

LIS INTRODUCTION. Line-intersect sampling has been used for measuring woody biomass of both living and dead trees, but is particularly common in the measurement of CWD biomass (e.g. Fahey *et al.* 1983; Sollins *et al.* 1987; Means *et al.* 1985, 1992; Arthur *et al.* 1993; Busse 1994; Feller 1987; O'Hehir and Leech 1997; Sturtevant *et al.* 1997; Pyle and Brown 1998, 1999; Chee 1999; Lindenmayer *et al.* 1999; Ringvall and Ståhl 1999a; Hély *et al.* 2000; Woldendorp 2000; Grove 2001; Currie and Nadelhoffer 2002; Bate *et al.* 2004; Keller *et al.* 2004b; Stevenson *et al.* 2006), both as logging residue and natural tree-fall. Line-intersect sampling involves sampling objects, in this case CWD, if they are intersected by a line transect (Ringvall and Ståhl 1999a, b), with the transect being of infinitesimally small width. The mathematics behind the line-intersect method is derived from probability theory. The greater the density of CWD, and/or the greater the length/width of CWD, the greater the probability of CWD pieces being intersected by the line-transect (Ringvall and Ståhl 1999a).

Warren and Olsen (1964) were the first people to apply the line intersect sampling method to estimate wood volume for a given area successfully. They concluded that a "plot", or transect, of narrow width would be more efficient than one with a greater

width, due to reduced searching time. They then expanded on the idea to the point where the transect had no width at all, and had effectively become a line. This line-transect only required CWD to be measured if it were intersected whilst traversing the transect, thereby reducing searching time to a minimum, as there was no need to measure CWD not intersected by the line. The design was originally intended to measure logging waste, and as such, is directly applicable to estimating CWD volume. This initial method required that the dimensions be measured for the CWD pieces intersected. However, van Wagner (1968) derived a formula allowing the line intersect method to be used where only the diameters of the CWD, where intersected by the line transect, needed to be measured. The formula accounts for the orientation of the CWD piece with respect to the direction of the line transect, and only the diameters at the point of intersection need to be measured.

One drawback of the line-intersect method, as described by Warren and Olsen (1964), is that it is sensitive to orientation bias, and a preliminary survey must be conducted before using this method. However, van Wagner (1968) states that if transects are run in more than one direction, the line-intersect method becomes robust to incidents of orientation bias. Bell *et al.* (1996) found that any orientation bias in logs can be accounted for by having a transect run in several directions. (See the following section *Correction for Bias in Orientation* (*Triangular Transect*), for a description of correcting for CWD orientation bias.) The multiple-direction transect design saves time by eliminating the preliminary orientation-bias test, as well as by making the quicker line-intersect method more available to surveys of CWD.

McIntyre (1953) recommends the use of the line-intersect method for heterogeneous stands of trees. However, if there are homogenous stands within a forest, this can be countered for by the random placement of transects (McKenzie *et al.* 2000) and adequate replication. The line-intersect method is also applicable for monospecific stands if the interest is for that particular species alone, as is usual with plantation logging residue.

Ringvall and Ståhl (1999a, b) were concerned that biased estimates may result from surveyors unconsciously moving toward or away from CWD pieces. However, if random directions are chosen then any potential bias toward, or away from, CWD will be eliminated. One method to achieve randomisation of transect directions is given by McKenzie *et al.* (2000), who recommended multiplying the seconds on a watch by three, and using this as your starting direction, in degrees.

McKenzie *et al.* (2000) recommend checking CWD density with a 25 m x 25 m plot before using the line-intersect method, and only using the line-intersect method if greater than 10 pieces of CWD are found in the plot. This creates extra work and wastes valuable time; negating the benefits of the line-intersect method. However, this preliminary plot-based check of CWD density appears unnecessary for two reasons. Firstly, there appears to be no reason for the 25 m x 25 m size of the plot. The size of the plot would have to be different for different CWD densities. This then would require a further preliminary plot-based check, with a plot of a different size. This would make the CWD survey extremely time consuming indeed, negating the time efficiency of using the line-intersect method. Secondly, there appears to be no valid reason for rejecting the efficacy of the line-intersect method for low density CWD (number of intercepts per hectare), so long as the starting lines is in a randomly chosen direction. Low number of interceptions can be accounted for by increasing transect length, or, by increasing the number of transects. It is recommended that the number of transects be increased, as this then maintains consistency in transect length, and maintains comparability between transects. If the CWD appears not to be in a uniform distribution, then several transects, each randomly placed and with a random starting angle, can be used.

Van Wagner and Wilson (1976) suggested that the number of intercepts needs to be sufficient to account for the variability in crossing logs at large ends, small ends, and central regions. Of course, the required number of intercepts will depend on the variability in the diameter size-classes of the CWD intercepted. If preliminary data is available, such as from a pilot-study, then the required total transect length can be calculated before commencing the survey. However, if preliminary data is not available then it would be safer to survey with multiple transects.

Brown (1971) developed a variant line-intersect method where the transect was in the form of a thin plane that had a given height above the ground, and only CWD that were intersected by this plane were included in the survey. Harmon and Sexton (1996), USDA Forest Service (2001), and Lutes (2002) state that all SDTs (standing dead trees) leaning with an angle of less than 45° from horizontal should be included in surveys of CWD. However, Lutes (2002) only measured CWD up to a maximum height of two metres above the forest floor. The obvious problem with this method is at what height do you stop including SDTs as CWD? The problems with decision-making, concerning inclusion or exclusion of CWD samples, are discussed by Ringvall and Ståhl (1999a).

CALCULATION OF CWD VOLUME. An estimate of CWD volume in the studied environment is required to estimate the mass of CWD, or any component of the CWD wood, in that environment (Woldendorp *et al.* 2002a). Van Wagner (1968) developed an equation where only the length of a line-transect and the diameters of logs intersected by the line-transect need be measured. The diameters are measured perpendicular to the central axis of the CWD piece, irrespective of the angle the transect line is intersecting the CWD axis. This equation provides an unbiased estimate of CWD volume providing that the pieces intercepted are (i) randomly oriented, (ii) cylindrical in shape, and (iii) lying horizontal on the ground. Points i and iii have been discussed above. The need for a cylindrical shape can be overcome if both the horizontal and vertical diameters (or maximum and minimum diameters) are measured. The horizontal and vertical diameters, measured during the CWD survey, can then be converted to an equivalent diameter by calculating the geometric mean of the two diameters (Harmon and Sexton 1996).

Van Wagner's (1968) equation for calculating the volume of CWD, per unit area, is:

$$V = \frac{\pi^2 \sum_i d_i^2}{8L}$$

Equation 2-6

Where: V = volume of wood per unit area (m^3 ha^{-1}),

d = piece (of CWD) diameter (cm) at the point of intersection, and

L = length of sample line (m) used in the survey.

The diameter of the CWD piece, d_i, is measured perpendicular to the central axis. If the diameter is being measured with diameter-callipers, then d_i^2 can be calculated as the quotient of the horizontal and vertical diameters. The equation can be modified as required to allow for other combinations of measurement units (O'Hehir and Leech 1997). If hollows are present in the CWD pieces, and the internal diameter of the individual logs, or branches, are known, then the formula can be modified to account for this (McKenzie *et al.* 2000). Additionally, if part of the 'circular' cross-sectional-area (CSA) is missing, then a representative diameter can be calculated based on the proportion of wood remaining from a 'theoretically-intact' CSA based on the measured diameters of each CWD piece. The calculation of CWD volume using different units of measurement is shown in Table 2-2.

Table 2-2. Calculation of CWD volumes using van Wagner's (1968) formula. Note the substitution of d^2 with individual horizontal and vertical diameters, as can be measured with diameter callipers. L is the length of the transect, in metres.

Dimensions of diameter measurements	Required CWD Volume ($m^3\ ha^{-1}$)	Required CWD Volume ($m^3\ m^{-2}$)
Diameter (cm)	$V = \frac{\pi^2 \sum_i (d_{i_h} d_{i_v})}{8L}$	$V = \frac{\pi^2 \sum_i (d_{i_h} d_{i_v})}{80000L}$
Diameter (m)	$V = 10000 \frac{\pi^2 \sum_i (d_{i_h} d_{i_v})}{8L}$	$V = \frac{\pi^2 \sum_i (d_{i_h} d_{i_v})}{8L}$

A CWD piece is only included in the transect survey if the transect intersects the central axis of the CWD piece (van Wagner 1968). If the transect runs along a log, but does not intersect its central axis, then the CWD piece is ignored. However, if the transect cuts across the end of a CWD piece, and crosses the CWD axis, then it is included in the survey, and the diameters measured perpendicular to the point of intersection (van Wagner 1968). Lucas and Seber (1977) suggested a method for including and excluding partially intersected logs, but this leads to the surveyors having to make decisions regarding the definition of 'partially intersected'. It is better to adhere to the recommendations of van Wagner (1968) and include logs whose central axes have been intersected by the line transect, and exclude logs whose central axes have not been intersected. If a line-transect intersects the axis of a single CWD piece more than once, then all intersections of the axis are to be included in the survey. Multiple intersections can occur if the piece is not straight, and is intersected more than once; such a situation is often encountered if a large branch is attached to a bole.

If a regional-survey is being conducted, where there is heterogeneity in ecosystems, then summary-statistics should be given for each different ecosystem type (Gale 2000). This prevents spatially-dominant ecosystem-types from 'swamping' smaller, and potentially rare, ecosystems. For example, if the majority of the region is dominated by an ecosystem type with low CWD-loadings (e.g. open woodland), averaging CWD loadings would ignore the rare (and possibly endangered) wet forests and closed forests which have high CWD-loadings; averaging CWD-loadings would result in

non-recognition of regional management-requirements for the maintenance of high CWD-loadings for these ecosystem-types.

CORRECTION FOR BIAS IN ORIENTATION (TRIANGULAR TRANSECT). If the CWD is not oriented randomly within a site, a single transect run in one direction may produce a biased estimate of the CWD volume (van Wagner 1968, 1982; Caza 1993; Woldendorp 2000; Woldendorp *et al.* 2002a). Non-random orientation of CWD can be the result of steep slope, windthrow, or anthropogenic activities during harvesting of trees (Woldendorp *et al.* 2002a). Kaiser (1983) stated that running line-transects in random directions can compensate for non-randomness of log orientation. Van Wagner (1968, 1982) stated that CWD orientation bias can be compensated for by averaging the results of transects run on more than one direction. The question to ask here is, 'how many directions'?

McKenzie *et al.* (2000) suggested running a single transect line in two perpendicular directions; the transect 'zigzags' in perpendicular directions until the required total length (≥20 m) is achieved, with both directions being of equal length. However, when orientation bias is an issue, van Wagner (1968), Bell *et al.* (1996), and Feller (1997) have shown that considerable errors can be made using a bi-directional transect design, although it is better than a uni-directional transect. They have found that a triangular transect with sides of equal length is superior to bi-directional transects, and is adequate to compensate for orientation bias in CWD. The equilateral-triangle line-transect was successfully used by Chee (1999) and Hély *et al.* (2000).

One issue with the triangular transect design, is the multiple crossing of a single CWD piece if it lies across one of the corners of the transect (van Wagner 1968). The rule to observe here, is that if the transect intersects the central axis of the log, then it must be included in the survey. If the transect intersects the central axis of the log twice, then the log should be measured twice, at each intersection. Any argument of overestimation with this technique is dispelled by the fact that the transect changed direction, and is just as likely to miss a second log that was just beyond the end of the former transect segment as it changed direction to the latter segment.

Van Wagner (1982) listed the following points as advantages of the equilateral-triangle design for the line-intersect transect:

"They can be of any size and number."

"Any single one will give a level of insurance against orientation bias that is obtainable only from a considerable number of randomly oriented sample lines."

"The starting points may be located without accurate surveying; i.e. the only measured distances necessary will be the sample lines themselves."

"The initial direction can be chosen at random or deliberately oriented to minimize (*sic*) an obvious orientation bias."

"The triangle need not be closed exactly as long as the lengths of the sides are accurately measured."

There are no major drawbacks to using the equilateral-triangle method, compared to other practical transect designs, therefore, it may be beneficial to use it at all times, regardless of the slope. Due to the fact that the surveyors return back to the starting point, with the equilateral-triangle method, there is less 'lost time' moving about when not sampling (e.g. returning to the starting point in the reverse direction that the transect was just run), making this method more time efficient than uni-directional or bi-directional transects (van Wagner 1968). (The triangular-transect is also quicker than the 'equivalent' three-separate-transects design, with each transect separated by 120°, as used by Currie and Nadelhoffer 2002; as the triangular-transect creates a single-path due to its loop-design.) The only possible transect design that would offer an appreciably greater improvement in CWD volume measurement, is a circular-transect. However, a circular design is impractical, as it would be difficult to walk in a circular direction. The triangular line-intersect transect is recommended as the best transect design for sampling CWD.

LENGTH OF TRANSECT REQUIRED. The final question to be answered is: what transect length is required to adequately sample the CWD for each forest type studied (van Wagner 1968)? Although the probability of intersecting a single CWD piece is proportional to its size (Watson 1971), the larger CWD pieces have a much lower frequency of occurrence (Harmon and Sexton 1996). The physical size of the larger CWD makes them more likely to be intercepted by a line transect than smaller CWD, but the lower stocking density of forests with larger trees creates fewer individual pieces of CWD for a given area. Since line-intersect sampling requires the intersection of an

individual piece of CWD for it to be included, and larger CWD is lower in density (individuals per given area) than smaller CWD, longer line-transects are required for assessing larger diameter CWD (Pickford and Hazard 1978). Unfortunately, there is no 'one solution fits all' answer to this problem, and the investigator is required to make this decision on available *a priori* data, or, if not available, then to make a subjective on-site assessment on the required transect length.

DISCUSSION OF PLOT-BASED VS LINE-INTERSECT TRANSECT DESIGN

Variability of decay within a single log (discussed in section 2.1.1.3 *Controlling Factors of Decomposition*) makes classifying a whole log problematic when using plot-based sampling, whereas the LIS method means that you only note the decay-state at the point of intersection by the line-transect.

The line-intersect method of surveying CWD is more time efficient than the plot-based methods (Warren and Olsen 1964; van Wagner 1968; van Wagner and Wilson 1976; O'Hehir and Leech 1997), which means that it is also more cost efficient (O'Hehir and Leech 1997). In a study, where surveyor accuracy was being checked in four sites, Ringvall and Ståhl (1999a) found that surveyor-induced bias is not a concern with line-intersect sampling, with the exception of one site with the highest density of logs. They found that the surveyors had a tendency to avoid logs in the stand with the highest CWD density. This problem can be avoided with diligent adherence to the straight-line direction of the transect segments. Randomisation of the initial transect direction should prevent bias in the first segment of the triangular line-intersect transect. Bias in the second and third segments can be avoided by standardising the directions for the second and third segments; e.g. always change direction in a clockwise direction (turn to the right).

2.2.6.2 Relascope Sampling of CWD

There has been some CWD sampling using the point relascope method and the transect relascope method (Gove *et al.* 1999, 2001, 2002; Ståhl 1998; Ringvall *et al.* 2001; Ståhl *et al.* 2002). These are angle-gauge estimations of CWD using plot-based and line-intersect methods respectively. The point relascope method uses an angle gauge or wedge prism to include or exclude CWD pieces, with the included pieces having their external dimensions measured with a relascope. The line-intersect transect relascope method is simply a method where CWD pieces intersected with a transect have their external dimensions measured with a relascope. This is a variant of

physically measuring the external dimensions with a tape measure. Unfortunately, the point method, which uses an angle-gauge, requires that the CWD be of a generally straight nature (Ståhl 1998). However, the eucalypts and rainforest trees of Australia do not produce branches that are straight in nature, although the boles are generally straight. Consequently, these angle-gauge methods are not applicable for the rainforests and eucalypt forests and woodlands of Australia if branch material is to be included in surveys of CWD (although they may have application in plantations of coniferous species).

2.2.7 LABORATORY METHODS

2.2.7.1 Determination of Sample Volume

There are two ways to determine the volume of a sample of CWD. Volume can be measured by the water-displacement method (e.g. Abbott and Crossley 1982; Fahey 1983; Barber and Van Lear 1984; Arthur *et al.* 1993; Brown *et al.* 1996; Chee 1999; Mackensen and Bauhus 1999, 2003) or calculated from the physical dimensions of the CWD piece (e.g. Stewart and Burrows 1994). Hereafter, 'sample volume' will refer to the volume of the sample as measured with the water-displacement method, and 'field sample volume' will refer to the volume calculated from the external dimensions of the CWD sample. Wood density calculated from the sample volume will yield the density of the wood in the sample, whereas density calculated from the field sample volume will result in a field wood density for the physical space occupied by the external dimensions of the CWD piece.

The overnight soaking of samples before water-displacement volume determination, as used by Erickson *et al.* (1985), standardises them at maximum saturation for volume determination. This standardises any 'swelling' effect, due to moisture content, to the maximum potential volume. This accounts for any variation in volume due to the rainfall regime immediately before sample collection, as well as for moisture loss from 'sample sweating' between sample collection and laboratory volume determination. Minimum volume, as could be achieved from drying the samples in an oven, prior to volume determination, is not a practical measure for wood volume for two reasons. Firstly, it is unlikely that larger diameter CWD pieces would be desiccated in the natural environment, as the inner wood is likely to retain some moisture. Secondly, it would be impossible to seal the smaller pieces (especially the fragmented 'rubble') without inducing errors by preventing water from entering pores in the porous material.

The impregnation of CWD samples with melted paraffin, to prevent water from entering the sample wood, was used by Barber and Van Lear (1984). However, this method is not recommended, as it may clog up air holes within the sample, and the subsequent water-displacement measurement of wood volume will erroneously include any air-pocket volume in the measurement of wood volume, which would lead to an overestimation of the sample volume.

When measuring the water-displacement volume, there are often small pieces of fragmented wood left in the container after soaking overnight. These small pieces of sample wood, which is common in fragmentary material, can be measured by placement in a plastic measuring cylinder, and water added to fill the measuring cylinder. The volume of the fragmentary pieces can then be calculated by removing the volume of added water from the volume of the measuring cylinder. The CWD piece volume is simply the sum of the piece volume and the volume of the fragments.

The calculation of field sample volume is used to determine the sample field wood density, which is used to measure the mass of the CWD in the field (with the use of the field CWD volume per unit area; e.g. m^3 ha^{-1}). Field sample volume requires the measurements of the wood diameter and sample disc thickness. The horizontal and vertical diameters should have been measured in the field when the sample was collected. Since these are the only diameter measured during transect surveys, there should be no further measurement of the diameter of the CWD disc. The thickness of the sample disc needs to be measured, and enough measurements need to be recorded to ensure a representative mean thickness is calculated for the sample disc. (The more irregular the thickness of the sample disc and/or the greater the circumference of the sample disc, the more measurements of disc thickness required to calculate a representative mean thickness.)

Sample volume (water-displacement volume) will usually be smaller than the field sample volume. However, it is possible for the sample volume to be greater than the field sample volume, especially in very dense or very dry samples. This is due to the field sample volume being calculated from field measurements; with ambient moisture content. However, the sample volume is measured on a saturated sample (to standardise the measurements), which will undergo some swelling during the saturation process. This may lead to the actual sample volume being greater than the field sample volume. Due to the greater amount of wood per volume in the samples with higher density, the higher density samples will swell to a greater amount than the lower density samples.

There is no standardisation of field sample volume, as CWD measurements in the field transect surveys are non-standardised. (That is, the CWD measured in the transect surveys is measured under prevailing conditions, and cannot be standardised for moisture content, therefore, the field sample volume is calculated in the lab without standardisation.).

2.2.7.2 *Determination of Sample Mass*

A range of drying temperatures has been used to dry CWD sample wood, ranging from 40 °C (e.g. Ganjegunte *et al.* 2004) to 105 °C (e.g. Christensen 1977; Edwards and Grubb 1977; Jurgensen *et al.* 1984, 1987, 1989; Erickson *et al.* 1985; Saldarriaga *et al.* 1988; Torres 1994; Delaney *et al.* 1998; Mackensen and Bauhus 1999, 2003; Tainter and McMinn 1999; Currie and Nadelhoffer 2002; Debeljak 2006; Bütler *et al.* 2007). The benefit of this temperature is that it is above the boiling point of water, and ensures that all water is removed from the samples; providing that they are dried to constant weight. Constant weight is defined as a weight loss of less than one percent between successive days weighing.

2.2.7.3 *Determination of Wood Density*

Sample wood density is calculated by dividing the dry mass by the sample volume (Fahey 1983; Barber and Van Lear 1984; Erickson *et al.* 1985). As wood density usually declines during the decay process (Erickson *et al.* 1985; Woldendorp *et al.* 2002a), sample density is the density that should be used to calculate decay rates of the CWD.

Field wood density is calculated by dividing the dry mass by the field sample volume, a method used by Arthur *et al.* (1993). Due to the external CWD dimensions being measured (horizontal and vertical diameters) during field volume surveys (line-intersect transect method), the field wood density should be used to calculate the mass of CWD in the field. The field wood density of the samples can be used to calculate a mean field wood density for each decay class of CWD, and this used to calculate the mean mass (per unit area; e.g. ha^{-1}) of wood in each decay class in the field. (The use of decay classes improves the accuracy of mass calculations for field CWD volumes (Busse 1994).) This calculation of field CWD mass is achieved by multiplying the field wood density of the decay class samples (g cm^{-3}) by the CWD volume in the field (m^3 ha^{-1}). (If using g cm^{-3} and m^3 ha^{-1}, the coefficient value will be in Mg ha^{-1}.)

2.3 CONCLUSIONS OF LITERATURE REVIEW

The conclusions of this literature review have been separated into the two broad categories that occur in the preceding sections. Namely, the first part is a conclusion of the general literature review, and the second part is the conclusions to the review of methods employed.

2.3.1 GENERAL CONCLUSIONS

The decomposition of CWD is a complex process that is predominantly the result of biotic degradation and removal of the wood-matrix. The rate of decomposition is determined by the chemistry of the wood-matrix, such as toxins, nutrients, and the relative proportions of labile and recalcitrant material. The rate of decomposition is also determined by the efficiency of the decomposer organisms, and the environmental conditions that influence their efficiency, such as temperature, available moisture, and whether the local-environment is aerobic or anaerobic. Population dynamics of the decomposer organisms is also important, such as the affects of predation, as this determines the actual amount of wood-matrix degraded or removed by the relevant decomposer organisms.

CWD has been found to be an important store for nutrients, which often accumulate during the decomposition process, and is especially important as a site for nitrogen-fixation by resident bacteria. This accumulation of nutrients means the contribution CWD makes to forest nutrient cycling increases with length of time the CWD resides on the forest floor.

Larger-diameter CWD has been found to contain the greater accumulations of nutrients, especially as nitrogen-fixation requires anaerobic conditions that are found in greater proportions in larger-diameter logs. Larger-diameter logs have also been found to provide greater structural complexity to ecosystem functioning than smaller-diameter logs; providing greater heterogeneity of habitat, and greater water-holding capacity in times of water-shortage. Larger-diameter logs may also provide better refuge-sites from environmental extremes such as desiccation and fire.

CWD is an integral part of ecosystems, and must be managed carefully if natural ecosystem functioning is to be maintained in forest environments. Allowing CWD amount to fall below natural levels leads to an impoverished environment as many components of the ecosystem are affected by the availability of adequate amounts of CWD.

2.3.2 REVIEW OF METHODS

The most common minimum-diameter threshold for separating CWD from fine-woody-debris is 10 cm, and this appears to have become the unofficial standard in CWD sampling, although there are occasions where other sizes can be justified (such as in ecosystems with very small or very large diameter source-trees). The five-class system of decay-classification has also become somewhat of a standard, with most researchers opting for five classes.

Sampling of CWD has traditionally been done by two methods, employing either direct-measurement of log-dimensions within plots, or by using the line-intersect transect (LIS) method; although some researchers have trialled using relascope sampling of CWD. The LIS offers a much faster method for measuring the volume of CWD, and, as such, for a given sampling time/effort allows the surveyor to cover a much greater area than can be achieved with direct-measurement plot-sampling. The triangular-transect, in the shape of an equilateral-triangle, is an adequate design to counter any orientation bias that may occur from trees falling in a non-random direction.

The chronosequence method has proven very popular with researchers, as it offers a quick method for assessing the progress of decay in CWD. The chronosequence method also allows completely independent selection of samples for each age category.

There have been many different decay-models used to describe the decomposition of CWD, but the single-exponential model (SEM) has proven the most robust and the most popular. The simplicity of the SEM means that minimal information is required from sampling techniques, it is less problematic when fitting to data, and is much easier to interpret than other more-complex models describing CWD decay.

Determination of sample wood-volume by the water-displacement method is very popular, and was the method chosen for this project. However, the sample must be soaked in water overnight prior to volume-measuring, with excess water drained immediately prior to processing, to prevent biased estimations of sample wood-volume. To allow for hollows, as is common in eucalypt CWD, volume calculated by external dimensions of the samples, which are then used to calculate 'theoretical densities', can be used to account for hollows when calculating mass of CWD in the field with the CWD environmental-volumes (as measured with line-intersect transect surveys). Measuring of sample-wood mass by heating to 105°C to constant mass has been popular, as the high temperature removes all non-structural components from the wood matrix; as all water and volatile compounds are removed.

Some methods used in this project have been developed within this project, as available techniques were seen to be inadequate for the sampling of eucalypt CWD. Such an instance was the need for the determination of a specific decay-classification system for eucalypt CWD (as shown in section 4.1 *Decay Classes of CWD*). A method of converting transect-lengths on sloping terrain to equivalent horizontal distances was also derived, as a flaw was detected in the existing method (see 3.4.1.4 *Correction for Slope*).

The findings of this review have been transferred into the methods used to sample CWD for this project. (See Chapter 3 *Methods* for discussion on the exact methods used for this project.)

CHAPTER 3

METHODS

This chapter describes the specific methods employed in this project; including methods of surveying CWD and sample collection in the field, laboratory-processing methods, and a brief description of the decomposition-model and statistical procedures employed. (Specifics of statistical procedures are given in the relevant sections of the Results chapter.) This chapter discusses several innovations used that have been developed to enhance existing procedures; such as a method correcting a flaw in the calculation of CWD-volume when correcting for the affect of slope, methods for describing orientation-bias and aspect parametrically (which allow them to be incorporated in multiple-regression analyses), and the derivation of a specific decay-classification method for eucalypts. This chapter initially describes the sampling sites, which are arranged along a latitudinal-gradient along eastern Australia, followed by a description of the decay-model employed in the analyses of the decay rates. The exact procedures used in the sampling and analyses of the samples collected follow the pattern of field sampling and surveying, laboratory sample-processing, and analyses of data.

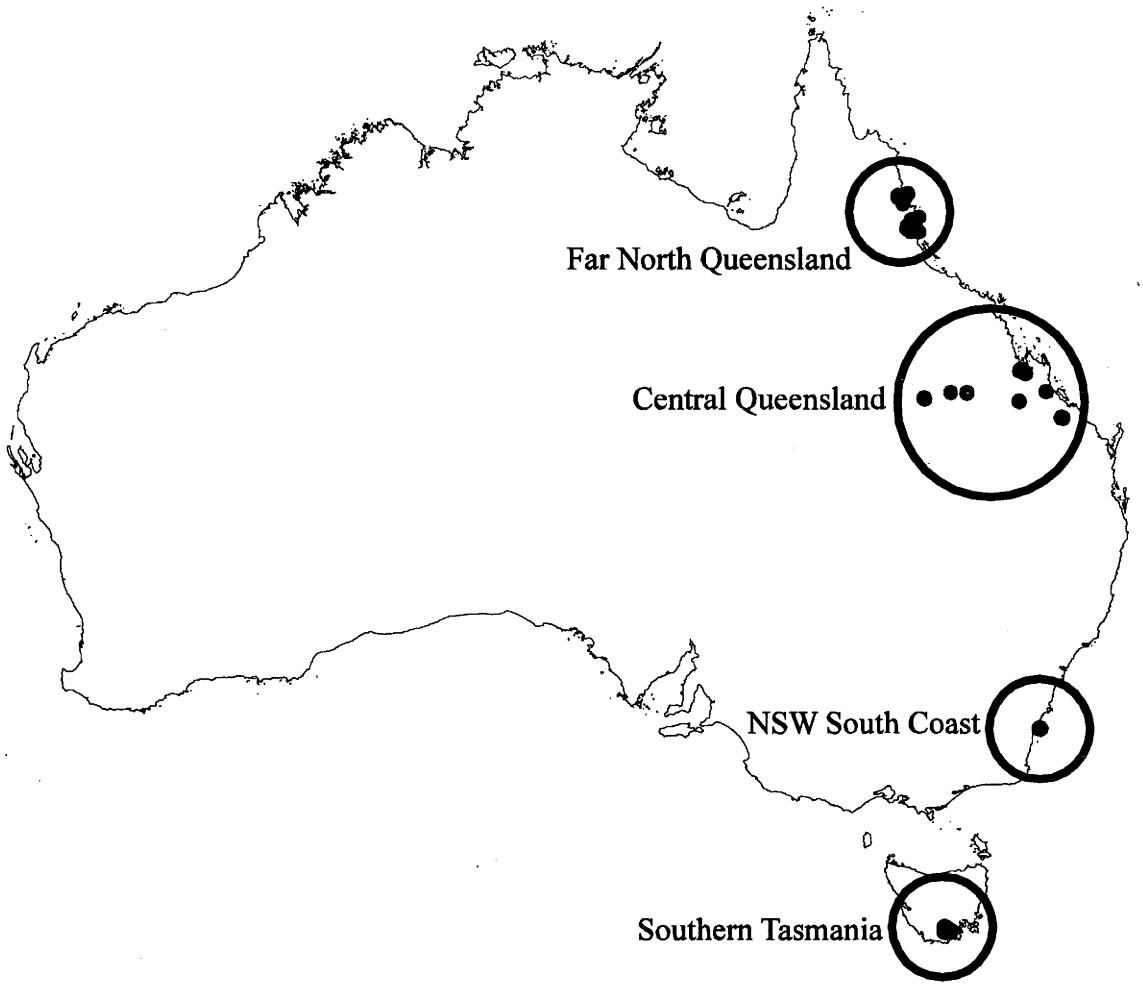
3.1 STUDY SITES

This study was carried out at four locations in eastern Australia (see Map 3-1). Wet eucalypt forest in southern Tasmania and the south coast region of NSW were sampled, along with dry eucalypt woodland in central Queensland and tropical rainforest in far northern Queensland.

The overriding criterion for choosing the sites surveyed in this project was the necessity to sample CWD of known age. Unfortunately, it has proven extremely hard to obtain information for eucalypt CWD older than twenty years, and this has led to the relatively disjointed nature of the sites selected.

The vegetation structure of each sampling region is shown in Figure 3-1. Note the trend of decreasing stem density from tropical rainforest to wet eucalypt forest to eucalypt woodland (Figure 3-1a). The greater variability in the Tasmanian wet eucalypt forests, compared to the wet eucalypt forests of NSW, is due to older (old-growth forest) and younger (more recently cleared) forests occurring in the Tasmanian sampling area. (The Tasmanian forests have been subjected to clearfelling, whilst the

NSW forests have generally been subjected to selective clearing in the past.) Note, however, that the median values shown for each region are very similar; with 557.5 stems ha^{-1} for Tasmania, and 568.3 stems ha^{-1} for NSW.



Map 3-1. Location of sampling and surveying sites in eastern Australia.

The basal areas (Figure 3-1b) show the wet forests (tropical rainforest and wet eucalypt forest) clearly greater than the eucalypt woodland of central Queensland. The low basal areas shown for the Tasmanian forests, creating the overlap with the woodland of central Queensland, are the result of young forests growing after clearfelling for commercial forestry. (Without the young forests for Tasmania included, there would not be any overlap between the wet forests and the eucalypt woodland regions.)

Rainfall and temperature values for the Far North Queensland plots are from historical data collected onsite by Commonwealth Scientific and Industrial Research Organisation (CSIRO) staff. Altitude measurements are also from CSIRO records

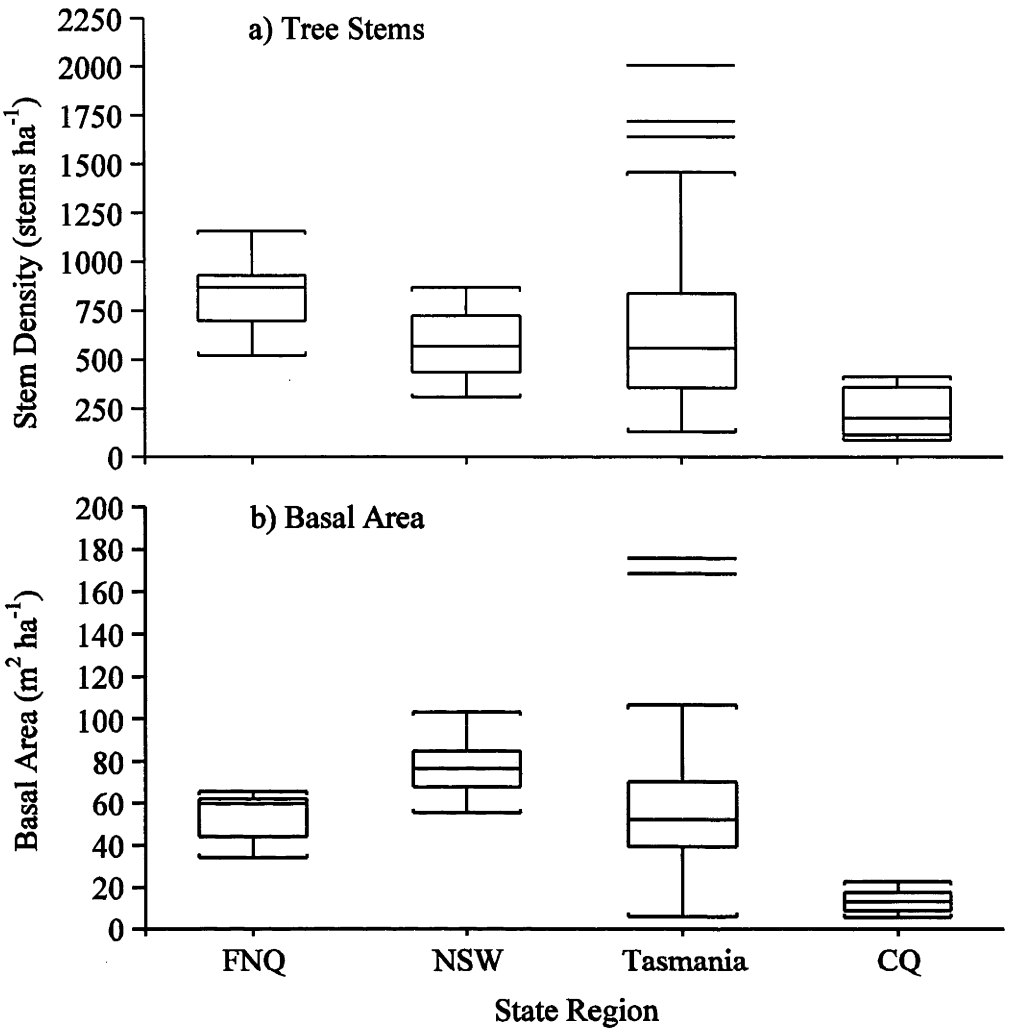


Figure 3-1. Stem density (a) and basal area (b) for far north Queensland (FNQ), New South Wales south coast (NSW), Tasmania, and central Queensland (CQ).

Rainfall and temperature values for the southern Tasmanian, NSW south coast, and central Queensland sample sites are from interpolations of Bureau of Meteorology climate records using the interpolation-software ANUSPLIN, from the Centre for Resource and Environmental Studies (CRES) based at The Australian National University. Altitude measurements for southern Tasmania and central Queensland were measured during sampling. The southern Tasmanian altitudes were measured on the road adjacent to the logging coupes, as all but the youngest regenerating forest was too dense for a GPS-unit to operate. Due to the often dense-nature of the NSW South Coast forest area, and many of the sites being away from roads, a GPS-unit could not be used for establishing altitude. For the NSW sites, it was decided that site-altitudes be obtained using the 9 Second Australian Digital Elevation Model, which provides 250 m

resolution, from the Centre for Resource and Environmental Studies (CRES) based at The Australian National University.

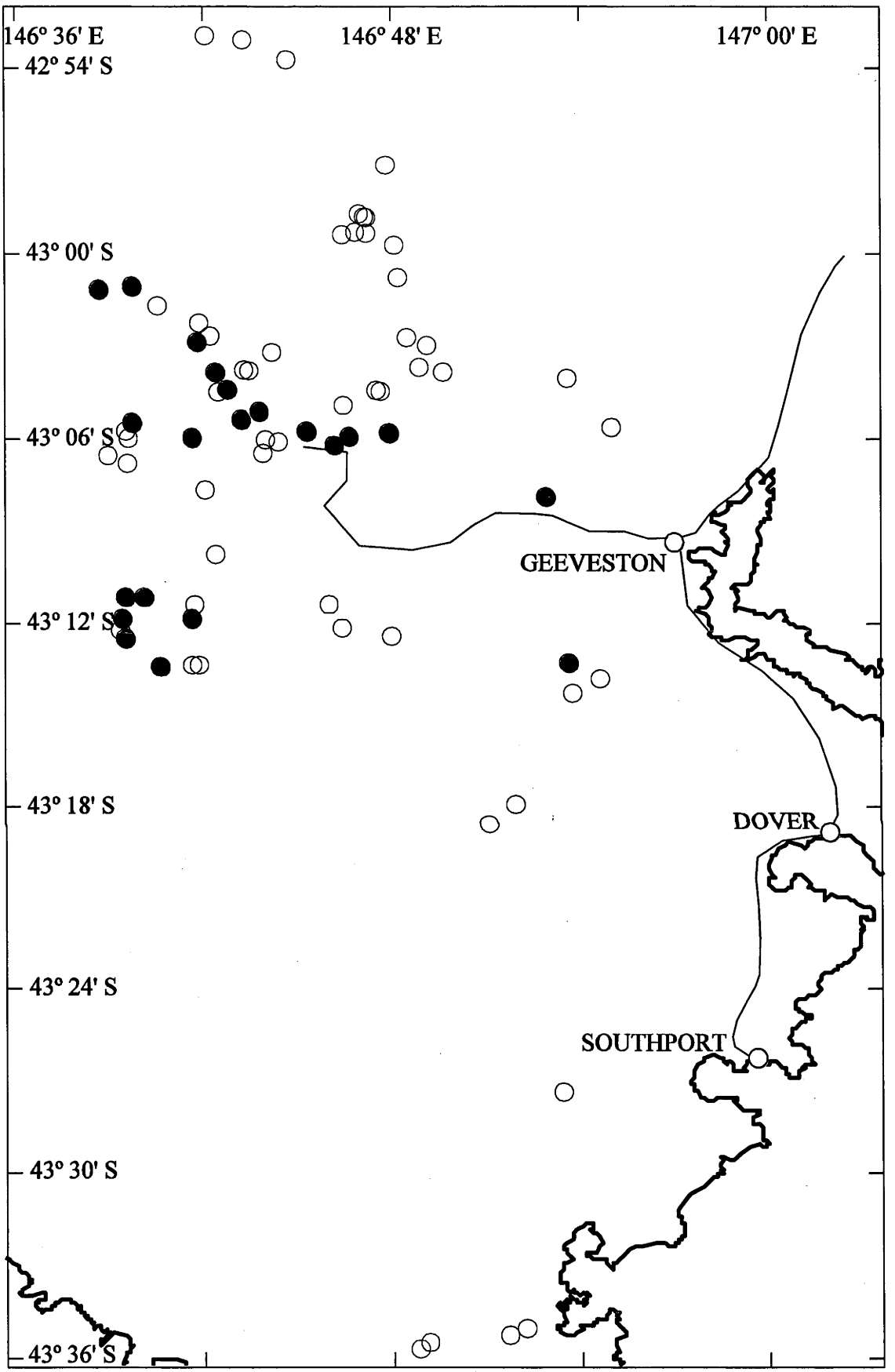
The ANUSPLIN interpolation and 9 Second Australian Digital Elevation Model values were supplied by the Cooperative Research Centre for Greenhouse Accounting; the author is a student member of the CRCGA.

3.1.1 SOUTHERN TASMANIA

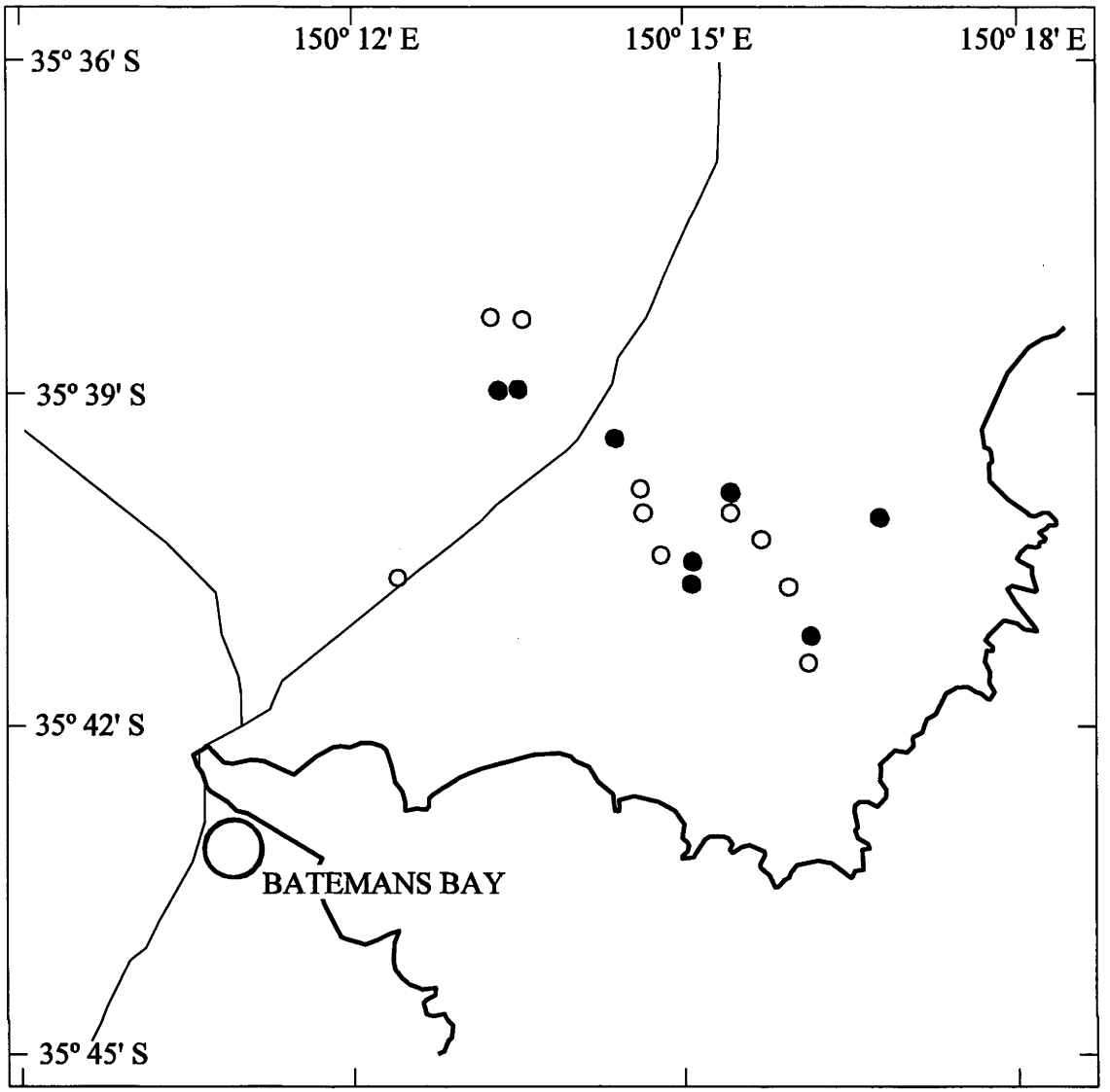
The sampling area is around and to the immediate west of the town of Geeveston in southern Tasmania (see Map 3-2). The sampling sites were in an area bordered by latitude 43° 01' S and 43° 13' S, and longitude 146° 39' E and 146° 54' E. Altitudes ranged from 74 m to 433 m, and site slopes ranged from 2° to 26°. The prevailing climate is cool-temperate with mild winters and mild summers. Mean annual temperature at the sites ranges from 8.2° C to 11.3° C, and mean annual rainfall ranges from 1024 mm to 1466 mm. The sampling was done in collaboration with Forestry Tasmania (FT), and all sampling was done of FT land. All samples were aged for the dates of logging of individual coupes. All sample sites logged post-1960 were subjected to a slash burn, while pre-1960 sites were not. However, the pre-1960 sites were subjected to forest fires since logging. The sampled sites were in stands of *E. obliqua*. No other species were sampled in Tasmania. Site locations are shown in Map 3-2. (The 53 transects for the study were done by FT field staff concurrent with the sample collecting and processing. Transects were not done at the sample sites, but were done within the area bordered by the sample sites.)

3.1.2 NEW SOUTH WALES SOUTH COAST

Sampling in southern New South Wales (NSW) was done in an area immediately to the north of Batemans Bay (Map 3-3). The sites are in an area formerly administered by State Forests of New South Wales (SFNSW) known as Benandarah State Forest. The sampling sites were in an area bordered by latitude 35° 38' S and 35° 41' S, and longitude 150° 13' E and 150° 17' E. Altitudes ranged from 22 m to 162 m, and site slopes ranged from 12° to 23°. The prevailing climate is temperate, with mild winters, and warm to hot summers. Mean annual temperature at the sites is steady at 16° C, and mean annual rainfall ranges from 1019 mm to 1065 mm.



Map 3-2. Location of sampling (●) and transect survey (○) sites in the wet eucalypt forests of southern Tasmania.



Map 3-3. Location of sample collection and transect sites (•), and transect-only survey (○) sites, in the wet eucalypt forest of southern NSW.

The seaward portion of Benandarah State Forest, to the east of the Princes Highway, was excised into an expansion of Murramarang National Park on the 1st January 2001, and is now under the administration of the National Parks and Wildlife Service of New South Wales. The portion to the west of the highway remains as Benandarah State Forest. A permit (No. 05618) was obtained for sampling in Murramarang National Park. Permission to sample in the SFNSW area was also obtained prior to sampling.

Historical records for all sampling sites, located at the SFNSW regional head office locate in the township of Batemans Bay, were used to age the samples collected. All sampled sites contained a mixture of eucalypt species. Site locations are shown in Map 3-3.

3.1.3 CENTRAL QUEENSLAND

Two dry eucalypt woodland species, *Eucalyptus crebra* F.Muell. and *Eucalyptus melanophloia* F.Muell., were sampled in an area from Rockhampton to just west of Alpha in central Queensland (Map 3-4). The geographical ranges of the sampling sites were from 22° 32' S to 24° 17' S, and 146° 01' E to 151° 07' E. Altitudes ranged from 116 m to 341 m, and site slopes ranged from 1° to 18°, with a flat to undulating terrain. The climate is subtropical, with warm winters and hot summers. Mean annual temperature for the sites ranged from 19.0° C to 22.7° C, with mean annual rainfall ranging from 490 mm to 940 mm.

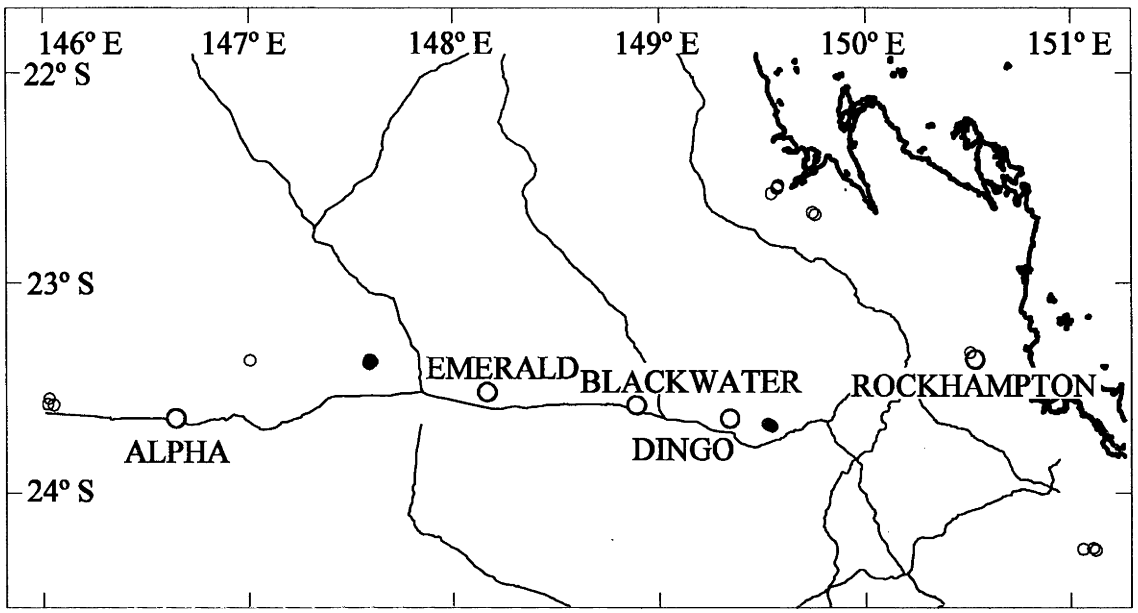
The sampling was done in collaboration with the Department of Primary Industries and Fisheries (DPI&F); Queensland Government. All sampling was done on privately held leasehold land used for pastoralism (cattle farming), and permission was obtained before sampling. Historical data was obtained from leaseholder records of land clearing for fence construction, and DPI&F records for inventory plots set up at three locations. All sites have been subjected to frequent low intensity fires, which are used to encourage the growth of new grass shoots. All of the sites sampled are shown in Map 3-4, and each site contained only one dominant eucalypt species (either *E. crebra* or *E. melanophloia*).

Most of the samples from central Queensland (*E. crebra* and *E. melanophloia*) were not collected from within woodlands, but were collected from cleared land adjacent to woodland, or from within cleared paddocks. The samples that were collected from woodland sites were beneath a canopy cover of 10-15%. A plot of the wood densities of the samples, stratified by canopy cover (cleared sites canopy cover = 0%) showed no difference in density for a given age. All samples collected from central Queensland are considered representative of the natural decay of the two species.

3.1.4 FAR NORTH QUEENSLAND

The sampling in far northern Queensland was in tropical rainforest, and was the only sampling not involving eucalypts. The sampling was in the region around the city of Cairns and the town of Atherton (see Map 3-5). The sampling region latitudinal range was 16° 08' S to 17° 31' S, and the longitudinal range was from 145° 04' E to 145° 46' E. The sampling area covered a range of rainforest subtypes, with some areas in rugged terrain. Altitudes ranged from 15 m to 1200 m, and site slopes ranged from 1° to 38°. The climate is moist tropical, with a distinct drier period from August to October. Mean

annual temperatures for the sites range from 18.9° C to 24.0° C, and mean annual rainfall is from 1403 mm to 3470 mm.



Map 3-4. Location of the sampling and transect survey sites (•) and sampling-only sites (○) in the dry eucalypt woodland of central Queensland.

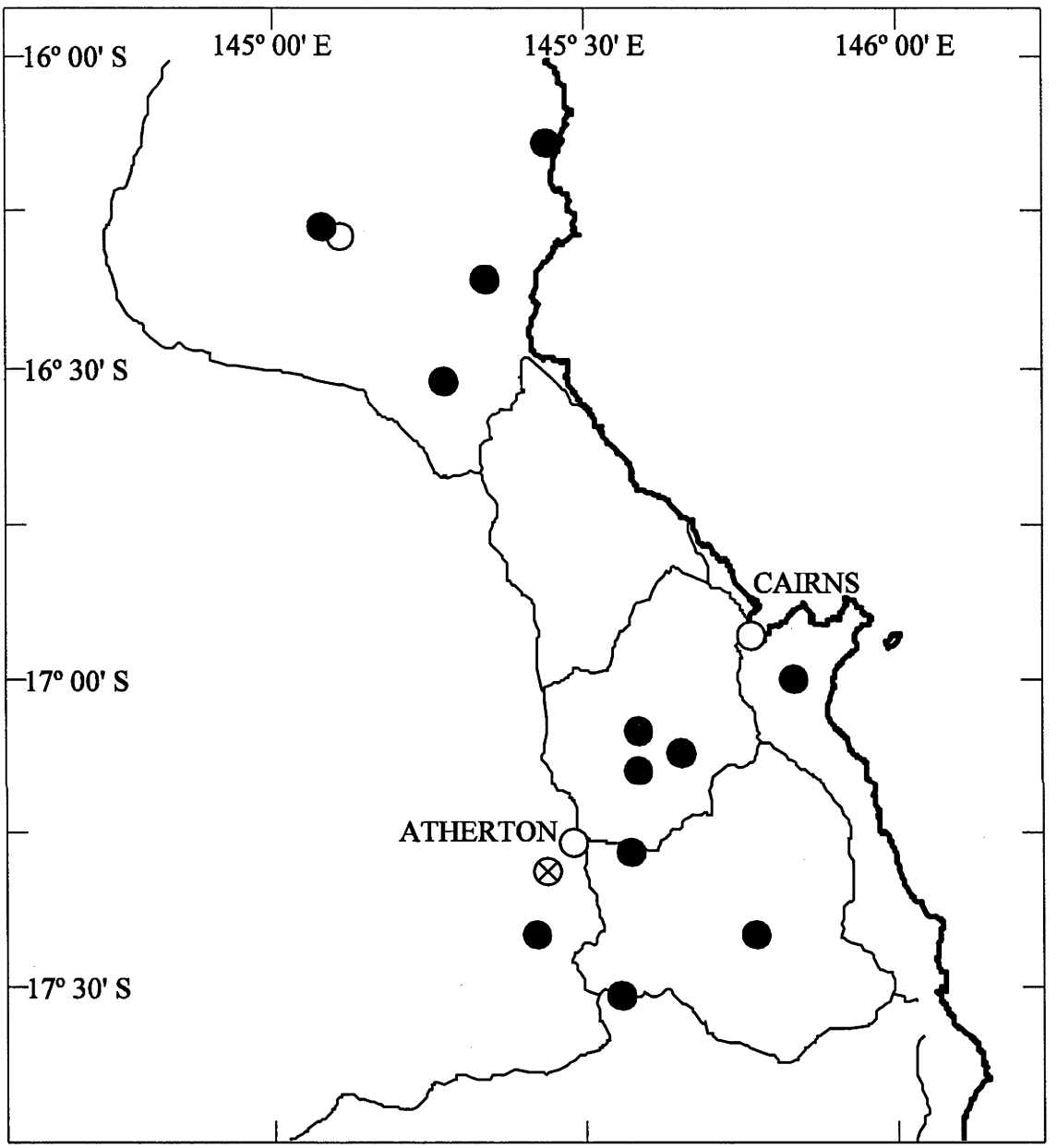
The sampling of the tropical rainforest was done in collaboration with the Tropical Forest Research Centre (TFRC) department of the Commonwealth Scientific and Industrial Research Organisation (CSIRO), located at Atherton. Sampling was conducted in freehold land as well as at locations in the Wet Tropics World Heritage Area. A permit was obtained by TFRC, for the duration of this project, to sample individual national park areas within the Wet Tropics World Heritage Area. (TFRC are the holders of the permit.)

Due to administrative problems encountered, only six of the 13 sampled sites were visited during the five-week stay of the author. After this period, the remaining seven sites were sampled by field staff of the TFRC.

Physical samples were only collected from sites within one kilometre from the nearest road, due to Occupational Health and Safety restrictions; the carrying of heavy equipment and samples over long distances in rugged terrain was considered dangerous. All sites greater than 1 km were surveyed for CWD volume only.

The number of samples collected from the sites varied considerably as the number of logs available at each site was variable, and the proximity of the site to vehicle varied

(the greater the distance from the site to the vehicle, the fewer trips available to collect and return samples).



Map 3-5. Location of the sampling and transect survey sites (•), transect-only site (○), and sampling-only site (⊗), in the tropical rainforest of northern Queensland.

3.2 DECOMPOSITION MODELS FOR CWD

3.2.1 SINGLE EXPONENTIAL DECAY MODEL OF CWD DECOMPOSITION

Coarse woody debris decay rates were calculated using the single-exponential model (SEM) of Olson (1963):

$$\frac{Q_t}{Q_0} = e^{-kt}$$ **Equation 3-1**

Where: Q_t = amount remaining at time = t,

Q_0 = initial amount, at time = 0,

k = decay model coefficient, and

t = time since death (CWD age).

This project used wood-density to determine the decay rates. Consequently, Q_t and Q_0 in the above model will become the relative density at time = t. That is, Q_t will be replaced with D_t, and Q_0 will be replaced with D_0, and D_t/D_0 is the relative density of the sample at time = t. The SEM is the most common model used to describe wood decay (Wieder and Lang 1982; Mackensen and Bauhus 1999, 2003; Mackensen *et al.* 2003). (See 2.2.5.8 Discussion — Comparison of Models, for the justification in employing this model to describe the decay dynamics of CWD.)

3.3 TYPES OF SAMPLING STRATEGIES FOR CWD

3.3.1 SIZE LIMITS OF CWD

This study uses the 10 cm minimum diameter threshold for both the collection of laboratory samples and field volume (transect) sampling. As a CWD-piece decays, its structural integrity is reduced and the CWD-piece can collapse due to the affects of gravity (Spies and Cline 1988). To account for this structural-collapse, a vertical and horizontal diameter-measurement was recorded; as *per* Næsset (1999b). The diameter measurements used are the geometric means of the horizontal and vertical diameters.

The length of the CWD to be sampled must also be considered, as decomposer organisms will colonise CWD from the ends as well as the surface (Leach *et al.* 1937; Harmon and Sexton 1996). Indeed, Laiho and Prescott (1999) found faster colonisation by decomposer organisms from the ends of wood than in the central-region. This study used a minimum CWD length of 1 m, where the sample taken was at least 0.5 m from any exposed end material.

3.3.2 DECAY CLASSES

Early stages of decay are characterised by a removal of bark and sapwood, with the latter stages of decay characterised by structural collapse of the CWD, all of which is visible to the human eye. However, the intermediate stages of eucalypt decay are

characterised by inner heartwood decay, with the observable outer heartwood remaining visibly unchanged.

Due to the lack of *a priori* density versus age data, and the pattern of eucalypt decay, where the intermediate stages of decay are characterised by internal change, an *a posteriori* system was devised to describe the CWD of the wet eucalypt forests by separate external-attribute parameter characterisation. Unfortunately, this system only includes the Tasmanian eucalypt data, as it was devised after the collection of samples and data from NSW. The *a posteriori* system was also used to devise decay class systems for the dry eucalypt woodland of central Queensland, and the wet tropical rainforest of far north Queensland.

Few CWD studies have linked substrate quality with field classification systems (Idol *et al.* 2001). Unfortunately, due to budgetary constraints, the determination of substrate quality (nutrient concentrations) was not performed in this project.

3.3.3 CHRONOSEQUENCE METHOD OF SAMPLE COLLECTION

This study uses the chronosequence method for the collection of samples for decay rate analyses. (For a thorough discussion of the chronosequence method see section 2.2.4 *Chronosequence and Repeated-Measures Studies*.)

The ages of samples for southern Tasmania and southern NSW were ascertained from logging records, while those for central Queensland were from pasture clearing records. The ages of samples for northern Queensland were calculated from inventory surveys, where the time of death was taken as the median age between consecutive sampling dates where the tree disappeared. The use of the median age for the northern Queensland samples is the same method as used by MacMillan (1981).

3.4 FIELD SURVEY METHODS

3.4.1 LINE-INTERSECT SURVEYS

During this project, the seconds of a watch were multiplied by 6 to obtain a random angle of up to 360°. Where transects were being run inside plots, and as a result, constrained by the plot boundaries, the random angle was used, but if it were to force the transect to exit the plot, the random angle was changed to the opposite direction. The reverse-direction method was also employed in areas that would have forced transects too near roads, as there would probably be an artificially high CWD incidence due to clearing along roads, and the pushing of felled trees into the forest adjacent to the

roads. This direction was used to establish the first-side of the survey-transect; that was designed as an equilateral-triangle.

Only CWD whose centre line (axis) were cut by the line-transect were included in the survey (as per BCMoELP and BCMoF 1998; Marshall *et al.* 2000; Woldendorp 2000; USDA Forestry Service 2001; Marshall and Davis 2002). If a CWD piece was cut more than once, then the diameters at all intersections were included, and measured.

This project did not use the planar intersect method (as per Brown 1971), but did include logs where portions were elevated slightly off the ground (usually because of locally undulating terrain). Elevated logs were also included when they were lying across other logs (where they would have been on the ground except for the occurrence of other logs preventing them from contacting the ground when they fell). All trees that were elevated, that is only the base of the tree was contacting the ground, were excluded from sampling, as they were considered to be standing dead trees (SDTs).

3.4.1.1 Calculation of CWD Volume

Calculation of CWD volume in the environment was made using the formula of van Wagner (1968). See Equation 2-6 (section 2.2.6.1 *Plot-Based Vs. Line-Intersect Surveys*) for a description of van Wagner's (1968) formula.

3.4.1.2 Correction for Bias in Orientation (triangular transect)

Compensation for CWD orientation bias was achieved with the use of an equilateral-triangle design for the line-intersect transects (van Wagner 1968; Bell *et al.* 1996; Feller 1997). The equilateral-triangle line-intersect transect was successfully used by Chee (1999) and Hély *et al.* (2000).

A check for the presence or absence of directional bias of CWD was achieved by measuring the angle of each CWD piece, the angle of the aspect at the site, and the slope of each site. A graph of the difference between the CWD direction and the aspect direction (called Δ-angle) was plotted against slope. If there is a directional bias due to slope, then Δ-angle should show a decreasing trend with increasing slope, as the trees could be expected to fall closer in the direction of aspect as slope increases (see Figure 3-2).

If the fallen trees were to roll once on the ground, they may end up being more oriented toward an angle perpendicular to the aspect; due to lodging against trees. In the event that there is a greater bias toward the perpendicular-to-aspect direction,

although unlikely, the triangular line-transect would also account for this bias. The triangular transect would account for any directional bias occurring in the CWD.

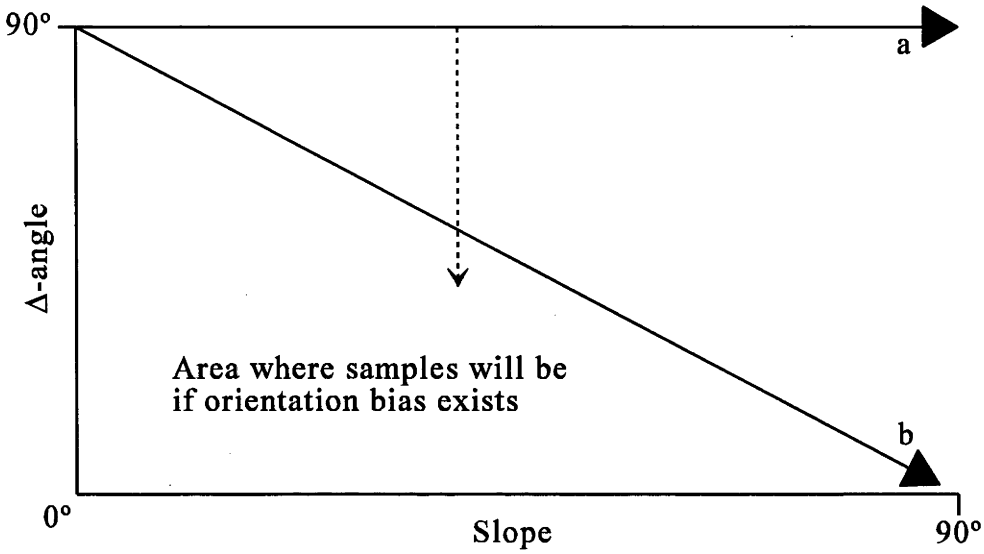


Figure 3-2. Check for orientation bias in CWD direction. If there is no orientation bias, then the Δ-angle values will be scattered evenly throughout (below line *a*). However, if an orientation bias does exists, then the values would all fall below line *b* (in the shaded area).

3.4.1.3 Length of Transect Required

Due to time and budgetary constraints, pilot studies at each location were impractical. Consequently, there was no indication of what length transects should be used in the surveys. It was decided that 300 m total length (100 m per segment) triangular transects would be sufficient, as it is longer than any multi-directional line transect encountered in the published literature. (As *a priori* data was unavailable, and as time and finance constraints prevented extensive interstate pilot studies of sites, it was decided that transects of length larger than in the literature would be appropriate in these often-modified landscapes).

However, due to the small nature of the inventory plots in the rainforest of northern Queensland (100 m x 50 m plots), the plots were segregated into two adjacent 50 m x 50 m plots, and a 150 m (total length) triangular transect run in each plot. This still resulted in a total length of 300 m of transect run (the triangles were still run at random angles within the plots; however, the starting point was at the nearest corner of the plot). This modification of the transect to remain within the survey-plots is akin to the strategy employed by Currie and Nadelhoffer (2002) where they had to break or stagger their transects to remain within plantations.

3.4.1.4 Correction for Slope (equivalent horizontal distance)

Van Wagner (1968) suggested that the affect of slope could be corrected by dividing the volume calculation per area covered by the "equivalent slope area". Unfortunately, this can lead to underestimations of CWD volumes with the line-intersect method, with the volume underestimation being greater with increasing slope. As an example, assume there is a uniform distribution of CWD, of uniform size. Using van Wagner's (1968) formula (see Equation 4.1), if we have a 100 m transect, with a Σd^2 of 4.863 m^2 (a Σd^2 of 0.4863 m^2 per 10 m), with a slope of 26°, then a 100 m transect run perpendicular to the aspect will have an equivalent horizontal distance (EHD) of 100 m, and will intersect a Σd^2 of 4.863 m^2 of wood. (There is no change in elevation over the transect length, therefore, there is no difference between transect length and EHD.) Whereas a 100 m transect run parallel to the aspect, will have an EHD of 90 m, and will intersect a Σd^2 of 4.377 m^2 of wood. If the horizontal conversion is left until after the volume calculations are done, then the conversion will be performed on two different volume values, with the second one having a value of only 90% of the actual CWD volume. However, if the EHD correction is performed prior to the volume calculation, then both volume calculations will show the same value, with both being correct. Therefore, it is imperative that the correction for slope be performed before the volume calculations are done! Consequently, it is important to have a formula that calculates the EHD before calculating CWD volume.

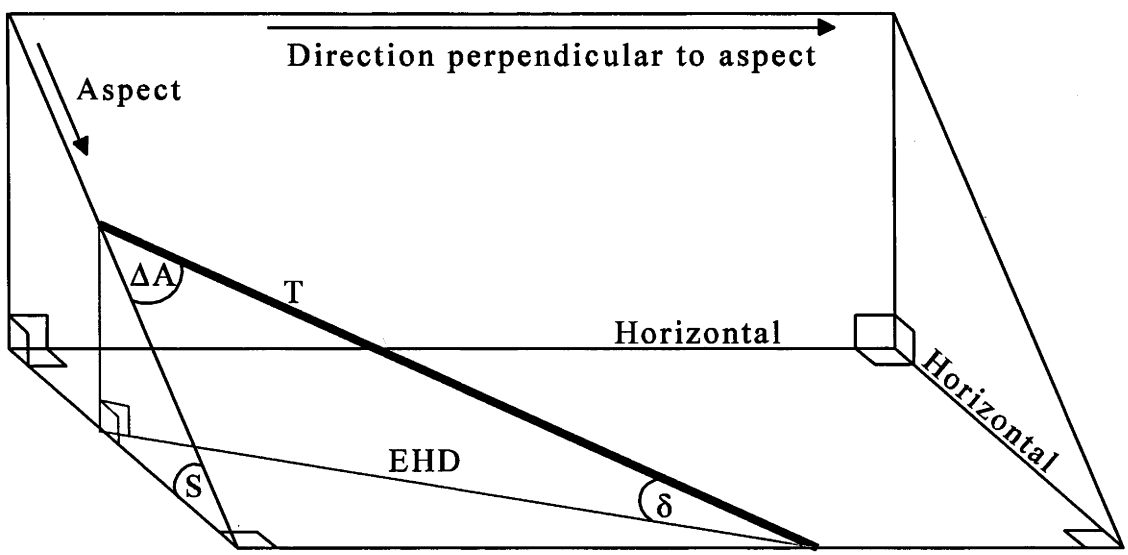


Figure 3-3. Diagrammatic representation of the varying affect of slope due to the random transect placement with respect to the aspect. T = transect, EHD = equivalent horizontal distance, S = slope of the terrain, and δ = effective slope of the transect. ΔA is the difference between the aspect direction and the transect direction.

Due to the slope of the hillsides surveyed, the 300 m transects may not cover 300 m in the horizontal plane (see Figure 3-3). Consequently, a method of calculating EHD's was necessary. Since transects are to be laid at random angles, the horizontal distance correction is not simply a matter of adjusting for slope, as transects are rarely run in the direction of aspect (directly downhill). It is possible to correct for slope in the field by holding a measured 'chain' horizontally, but this often requires the removal of interfering foliage from low vegetation; and the removal of low-foliage is not permitted when working in nature parks and reserves. The slope-correction method allows *post hoc* adjustment for slope, which does not require the manipulation or removal of vegetation.

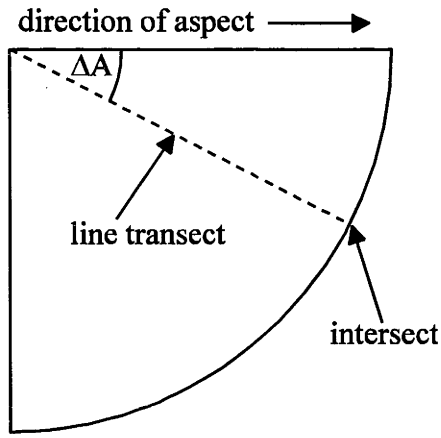


Figure 3-4. The deviation of the direction of the line-transect from the aspect can be thought of as existing within a quadrant of a circle. ΔA is the deviation of the direction of the line-transect from the aspect direction.

All possible angles of deviation of transect direction from the aspect direction can be calculated by using a single quadrant of a circle, with the aspect on one axis, and the perpendicular direction (the maximum deviation of the transect direction from the aspect) on the other axis. (The range of possible deviation angles, 0° to 90°, of the transect from the aspect, is contained within the quadrant.) The length of the transect line can be found by calculating the length of the line, from the origin to the line-arc intersect (see Figure 3-4).

As the angle of the slope increases, the horizontal area swept by the transect becomes shorter in the direction of the aspect. However, the distance perpendicular to the aspect remains stable. This effect changes the shape from that of a quadrant of a circle to that of a quadrant of an ellipse (see Figure 3-5).

The affect this has on the transect length is quite complex, as it is being affected by the changing length of the axis in the direction of the aspect, but a stable perpendicular axis length.

Figure 3-6 shows the complexity of the EHD. Therefore, a means of compensating for slope of the terrain, which accounts for the direction of the line-transect with respect to the aspect direction is necessary.

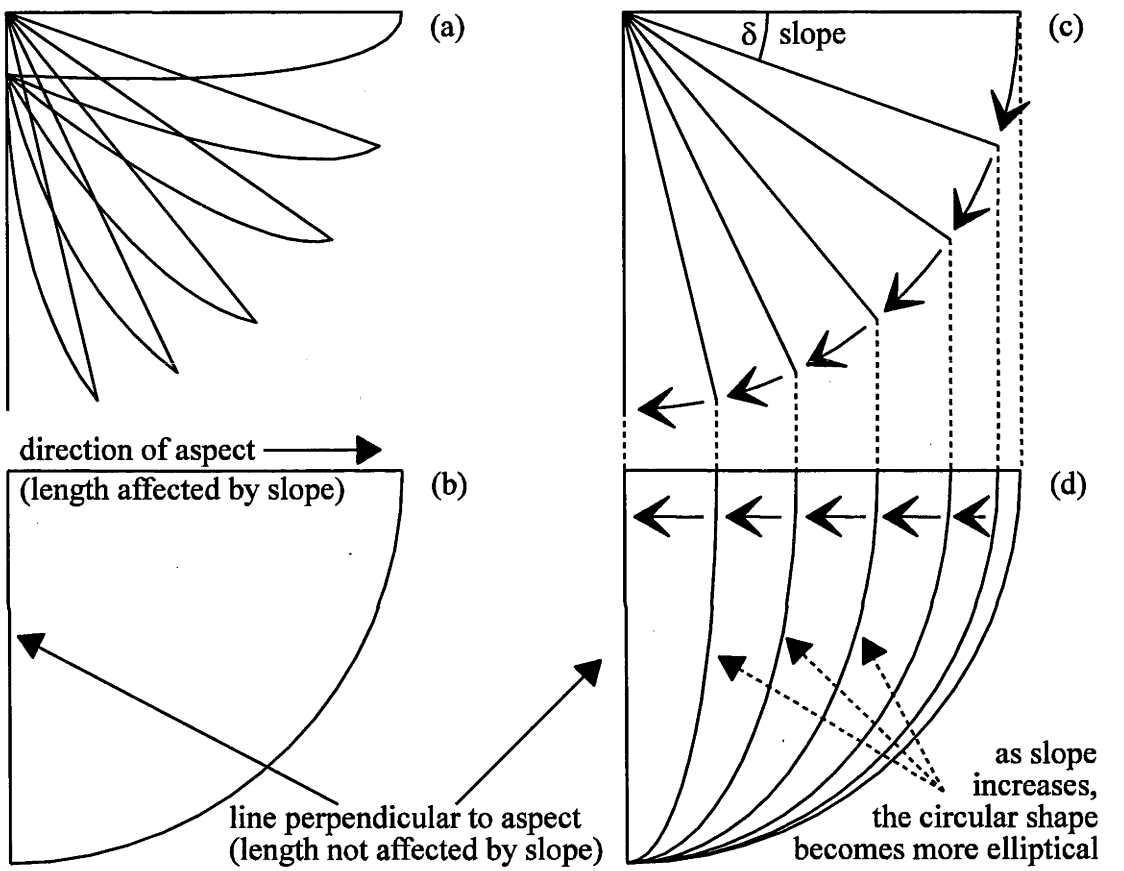


Figure 3-5. (a) is the swept-area quadrant as it is affected by slope, (b) is the horizontal equivalent area (shadow) formed by the quadrant, which is circular when the slope = 0, (c) is the side view of the quadrant as it is affected by slope, and (d) is the elliptical shape formed by the quadrant as it is affected by increasing slope. δ is the angle of the slope.

Although it is possible in many circumstances to hold a tape-measure horizontally for a short distance (e.g., 10 m segments), and measure horizontal distance in the field, this is not always possible; especially in forests with thick ground vegetation.

The underlying theory and mathematical proof for the correction of this problem can be seen in Appendix B. Presented here is the formula for the conversion of

traversed-distance to horizontal-distance, for either a single-direction line-transect or a single transect segment.

$$EHD = \sqrt{\frac{T^2.\cos^2 S}{\cos^2 S.\cos^2(90° - \Delta A) + \sin^2(90° - \Delta A)}}$$ **Equation 3-2**

Where: T = the length (m) of the transect (or transect segment),

S = the slope (°) in the direction of aspect,

ΔA = the deviation of the transect direction from that of the aspect (°).

For the purposes of calculator or computer use, the following interpretation of the above formula may be easier to use:

$$EHD = \sqrt{\frac{T^2.(\cos S)^2}{(\cos S)^2.[\cos(90° - \Delta A)]^2 + [\sin(90° - \Delta A)]^2}}$$ **Equation 3-3**

If on-site correction is desired, so that the horizontal-distances are all of the same distance, this formula can be used to construct a correction-table for field usage.

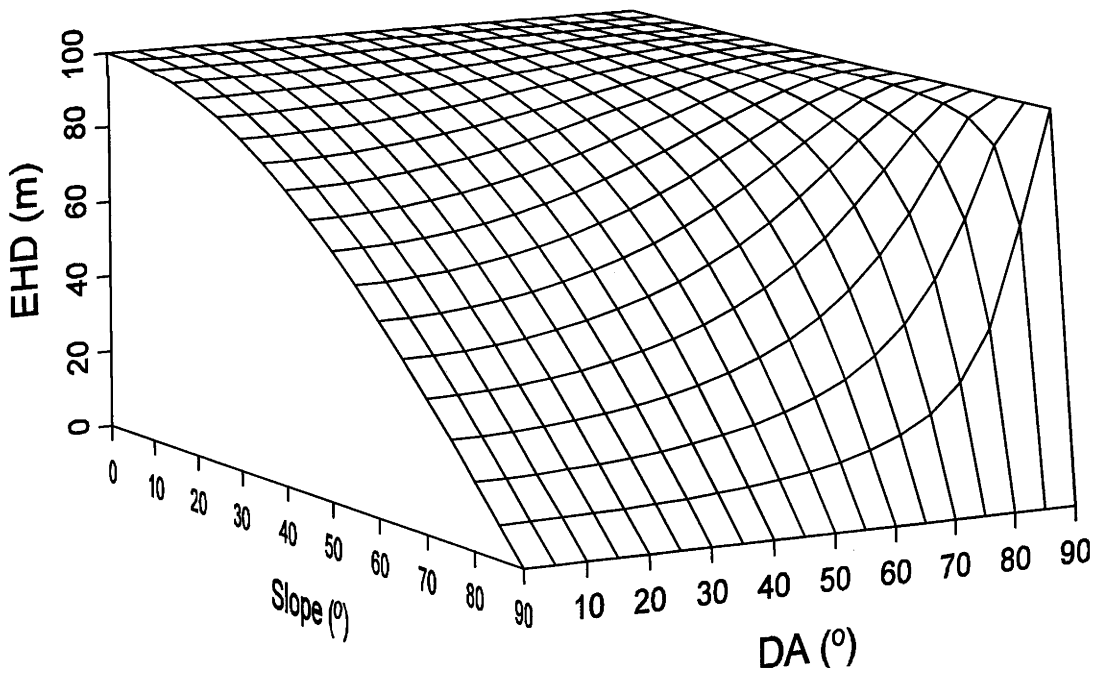


Figure 3-6. Equivalent horizontal distance (EHD, in metres) of 100 m transect as a function of slope (°) and the deviation of the transect direction (°) from the aspect direction (°).

3.4.1.5 Correction for Aspect

A method for aspect enumeration was developed for use in the statistical analyses. A description of the method developed can be found in Appendix A. This method is based on the aspect angle from the equator, with the aspect facing the equator having the lowest numerical value, and the aspect facing the pole (north or south) having the highest numerical value. This method has been chosen in order to make the enumeration complimentary to latitude and altitude; lowest values for aspect, latitude, and altitude, are expected to provide the best conditions for decomposition, and forest growth. (This method is suitable for enumerating aspect for its affect on forest growth, as well as for CWD decomposition.)

Although all sampling in this project was done in the southern hemisphere, this system was used to combine like-with-like aspects (e.g. NW and NE aspects). The conversion formula used is the southern hemisphere formula:

$$A_{dec} = 9 - \frac{|A_{deg_S} - 180|}{22.5}$$ **Equation 3-4**

Where: A_{dec} = parametric-aspect,

A_{degS} = direction (in degrees) for southern hemisphere readings,

| | = absolute value.

3.5 LABORATORY METHODS

3.5.1 COLLECTION AND STORAGE OF SAMPLES PRIOR TO ANALYSES

Wood samples were removed from the CWD using a chainsaw for solid wood, and a pruning saw for samples comprising lower-density wood, as per the recommendations of McKenzie *et al.* (2000). The samples were collected in the form of a disc (McKenzie *et al.* 2000), with a disc-thickness ranging from four to eight centimetres. (Busse (1994) used a minimum thickness of four centimetres, while Krankina *et al.* (2002) used 2-5 cm thick discs.) The majority of samples had a diameter between 10 cm and 35 cm; this size range was chosen as it allowed a greater number of samples to be dried in the available oven space for the duration of the on-site field sampling. Larger diameter CWD (up to 1.9 m in southern Tasmania) was sampled by cutting a wedge from the side of the log; with the point of the wedge originating at the centre of the log; cutting wedges from larger logs is the same strategy employed by Feller (1997). (Due to the size of these logs, it was impractical to cut a sample from the underside, so a wedge was

cut from the side of the log, as this was assumed more representative than a sample cut from the top of the log.) All samples were placed in plastic bags (Abbott and Crossley 1982) and kept in dark conditions during transport back to the laboratory.

The samples for density determination (volume and mass measurement) were processed immediately upon return to the laboratory. All of these samples were processed in laboratories close to the collection sites, with the exception of the southern NSW samples which were transported back to ANU (Canberra, ACT).

3.5.1.1 Determination of Sample Volume

Sample volume was measured in the laboratory by two methods (i) volume-displacement of water — to be used to measure sample wood-density, and (ii) volume calculated from external dimensions of the sample disc (diameter and thickness) — used to calculate theoretical-density for the space occupied by the external dimensions of the sample-disc. (To allow for hollows, as is common in eucalypt CWD, volume calculated by external dimensions of the samples (which includes hollows), can then be used to calculate 'theoretical densities' — this theoretical density can be used to account for hollows when calculating mass of CWD in the field with the CWD environmental-volumes; as measured with line-intersect transect surveys.)

See section 2.2.7.1 *Determination of Sample Volume* for a thorough discussion of the philosophy behind the decision to use these methods.

3.5.1.2 Determination of Sample Mass

The samples for density determination were dried in ovens at 105°C until a constant weight was achieved, with the exception of the southern NSW samples, which were dried to constant weight at 75°C. Constant weight is defined as a weight loss of less than one percent between successive days weighing. Due to the large size of the samples, the mass was recorded to the nearest gramme; some samples had a mass exceeding 15 kg. Dry mass is also used for the determination of theoretical wood density, as it is the mass of wood that is required; not the mass of wood and residual water.

3.5.1.3 Determination of Wood Density

Sample wood density is calculated by dividing the dry mass by the sample volume (Fahey 1983; Barber and Van Lear 1984; Erickson *et al.* 1985). As wood density usually declines during the decay process (Erickson *et al.* 1985; Woldendorp *et al.*

2002a), sample density is the density that should be used to calculate decay rates of CWD.

Theoretical wood density is calculated by dividing the dry mass by the field sample volume, a method used by Arthur *et al.* (1993). Due to the external CWD dimensions being measured (horizontal and vertical diameters) during field volume surveys (line-intersect transect method), the theoretical density should be used to calculate the mass of CWD in the field. The theoretical density of the samples can be used to calculate a mean theoretical density for each decay class of CWD, and this used to calculate the mean mass (per unit area; e.g. ha^{-1}) of wood in each decay class in the field. (Use of decay classes improves accuracy of mass calculations for field CWD volumes (Busse 1994).) This calculation of field CWD mass is achieved by multiplying the theoretical density of the decay class samples (g cm^{-3}) by the CWD volume in the field (m^3 ha^{-1}). (If using g cm^{-3} and m^3 ha^{-1}, the coefficient value will be in Mg ha^{-1}, or tonnes ha^{-1}.)

Idol *et al.* (2001) measured the density of the outer wood (bark and sapwood) and inner wood (heartwood) separately for decay classes II and III (they used a 5-class system) of CWD in three USA oak and hickory dominated forests. Unfortunately, it is not always easy to distinguish between sapwood and heartwood in eucalypt species, and this method may have limited use in analysing eucalypt species. No attempt was made to determine the density of the separate components of the sampled wood, and the density values reported here are for the entire sample disc collected.

3.6 STATISTICS

3.6.1 STATISTICAL PROCEDURES

All statistical analyses were performed using S-PLUS 6.1 (Insightful Corporation). A level of significance of $\alpha = 0.05$ was used throughout.

Single exponential decay model values were determined with the use of the S-PLUS *nls*-function (non-linear least squares regression). Model comparisons were made using the *nlme*-function (non-linear mixed effects models). Decay was modelled against sample site physical and climate parameters using multiple regression analysis.

Modelling of CWD contribution to forest carbon accounting (Discussion Chapter) was done with Mathcad 2001 (MathSoft Engineering & Education, Inc 2001).

A decay class system for wet eucalypt forests was established using cluster analysis, with the non-hierarchical *pam* (partitioning around medoids) function (Struyf *et al.* 1997; Insightful Corporation 2001). This system was devised using *E. obliqua* from southern Tasmania. The need for the classification system was established after problems classifying the NSW samples, and, therefore, NSW was not classified, nor used, in the derivation of the classification system. Although the classification system was based on a single species of eucalypt, there were no noticeable differences in the parameters used between the eucalypts of southern Tasmania and those observed when sampling in the wet eucalypt forest of NSW. (See Appendix C for a description of the methods used to define the decay class systems.)

The determination of orientation bias was checked by graphing the difference in direction between aspect and the CWD piece against slope. If an orientation bias exists, then the difference in angle should decrease as slope increases; the existence of such a trend would provide evidence of an orientation bias in CWD direction, and necessitate the use of line-transect designs to compensate for the bias.

3.6.2 PSEUDOREPLICATION

Unfortunately, due to the paucity of reliable time-since-death (how old the CWD is) data, the lack of available replicate sites resulted in a measure of pseudoreplication that was unavoidable. Spatial restrictions also led to pseudoreplication in southern Tasmania, where the Warra-grant conditions restricted sampling to the Warra LTER area and the immediate surrounding area; replicate sites could not be sourced from other areas. Unfortunately, the requirement for accessing samples where the age is accurately known is a restrictive constraint when studying CWD decay dynamics (Næsset 1999b). The occurrence of unavoidable pseudoreplication is one that is encountered occasionally in observational ecological studies; for a discussion of pseudoreplication, see Hurlbert (1984).

CHAPTER 4

RESULTS

The results of the data-analyses of field-surveying and sample-processing are presented in the order of decay classes of CWD sampled, decay rates, amount of CWD in the environment, multiple-regression analyses, and orientation-bias of CWD with respect to slope. Although general information regarding the methods of decay-modelling and statistical analyses are given in the previous chapter, any project-specific methods used in the analyses of data are provided in the relevant sections of this chapter.

4.1 DECAY CLASSES OF CWD

4.1.1 DETERMINATION OF DECAY CLASSES

The cluster analyses for the decay classes used the non-hierarchical *pam* (partitioning around medoids) function (Struyf *et al.* 1997; Insightful Corporation 2001). The analyses were done on coding of CWD external parameters (see Appendix C for a thorough explanation of the coding method used). The use of external-characteristics affords rapid assessment of a log's decomposition state (Pyle and Brown 1998).

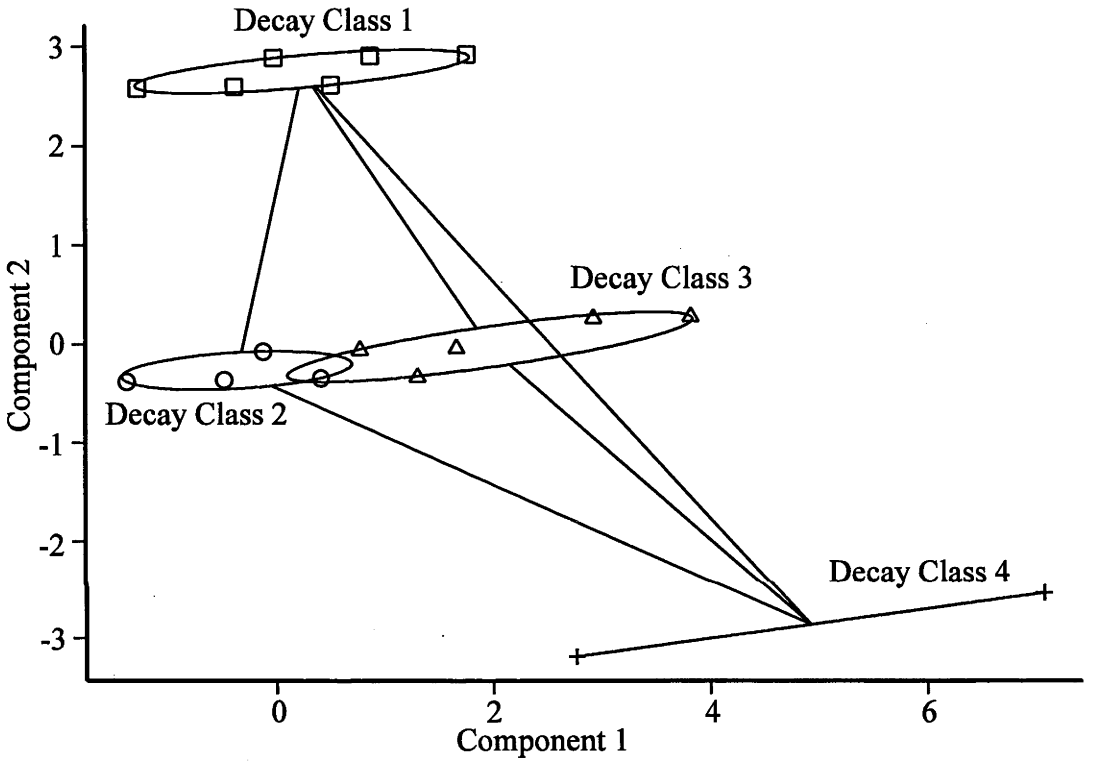
The analyses comprised testing each forest type with analyses running different number of groups. The most appropriate number of decay-class groupings was determined from the analyses, by inspecting the output for the most 'logical' grouping set. All samples (except NSW samples) were then placed into the relevant decay classes.

The analyses output was then used to construct 'decision-trees', which affords rapid determination of sample decay-class in field studies. This method eliminates potential conflicts between decay classes, where a particular CWD piece has some attributes belonging to one class, and other attributes which belong to another class. The decision-trees have been constructed in such a manner, that they are only used until a recommended decay class is encountered; you only continue through the decision-tree for as long as it takes to classify the CWD piece.

4.1.1.1 Southern Tasmania

The maximum number of decay-class groups recommended by the cluster analyses was four, as the five-class analysis produced an unstable output; different samples of the

same coding were being split between two groups. (See Figure 4-1 for the graphical output of the four-group analysis.) However, the eucalypt samples (*E. obliqua*) used for this analysis did not include the most decayed class, where the CWD is made up of rubble (collapsed and fractured); as there were no samples of this class available for collection (only samples of known age were collected). This missing class was appended to the four classes recommended by the analyses, to produce a five-class system to describe the eucalypt CWD. The decision-tree for the five-class decay-state system for the eucalypt samples can be seen in Table 4-1.



These two components explain 64.21 % of the point variability

Figure 4-1. Recommended cluster analysis output for *E. obliqua* samples, showing the four recommended groups of decay classes (n = 128).

Table 4-1. The 5-group decision-tree of decay classification developed from cluster analysis of *E. obliqua* samples.

PARAMETER	QUESTION	DECISION	
		YES	NO
Shape	Is the log rubble on the ground?	Class 5	continue
	Is the log flattening out?	Class 4	continue
Bark	Is there any bark remaining?	Class 1	continue
Cracks	Is the log splitting apart?	Class 3	continue
	Is the sample devoid of any cracks?	Class 2	continue
Log Density	Is the log solid (not soft/porous)?	Class 2	Class 3

4.1.1.2 New South Wales South Coast

As the coding system required for the cluster analyses was not in use when the NSW sampling was done, there is no cluster analysis for the NSW samples. (See section 3.6.1 *Statistical Procedures* for an explanation.)

Although the wet eucalypt forest classification-system was based on a single species of eucalypt in southern Tasmania (*E. obliqua*), there were no noticeable differences in the parameters used between the eucalypts of southern Tasmania and those observed when sampling in the wet eucalypt forest of NSW. It is therefore considered acceptable to use the classification system derived for the wet eucalypt forests of southern Tasmania in future sampling of southern NSW wet eucalypt forests.

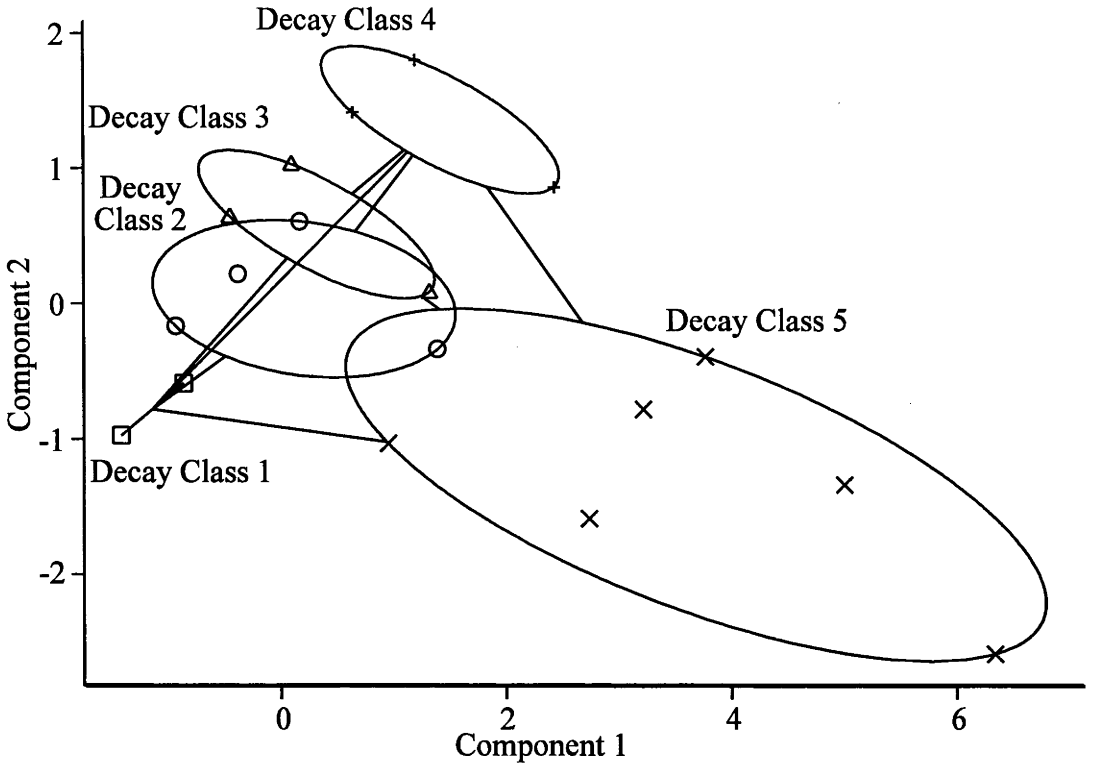
4.1.1.3 Central Queensland

The cluster analyses of the dry eucalypt samples, from subtropical central Queensland, produced results that suggested three-, four-, or five-class systems could be used. The five-class system was adopted as the most appropriate, as it afforded a greater distinction between groups than the three- and four-class systems, and was still stable. The analyses were performed on 93 samples comprising two eucalypt species (see Figure 4-2). The five-class decision-tree derived from the cluster analysis is shown in Table 4-2.

Log density was not useful in distinguishing between the decay classes of the dry woodland samples. This is undoubtedly a result of the extremely slow decay rate of the dry-woodland species studied, where most loss is from fragmentation of lower density wood. (See section 4.2 *Decay Rates* for further discussion.)

Table 4-2. The 5-group decision-tree of decay classification developed from cluster analysis of dry woodland *E. crebra* and *E. melanophloia* CWD samples.

PARAMETER	QUESTION	DECISION	
		YES	NO
Shape	Is the log shape intact (not flattening)?	continue	Class 5
Bark	Is the bark incomplete (some missing)?	continue	Class 1
Cracks	Are there deep cracks into the interior of the wood?	continue	Class 4
Bark	Is there any bark remaining?	Class 2	Class 3



These two components explain 90.52 % of the point variability

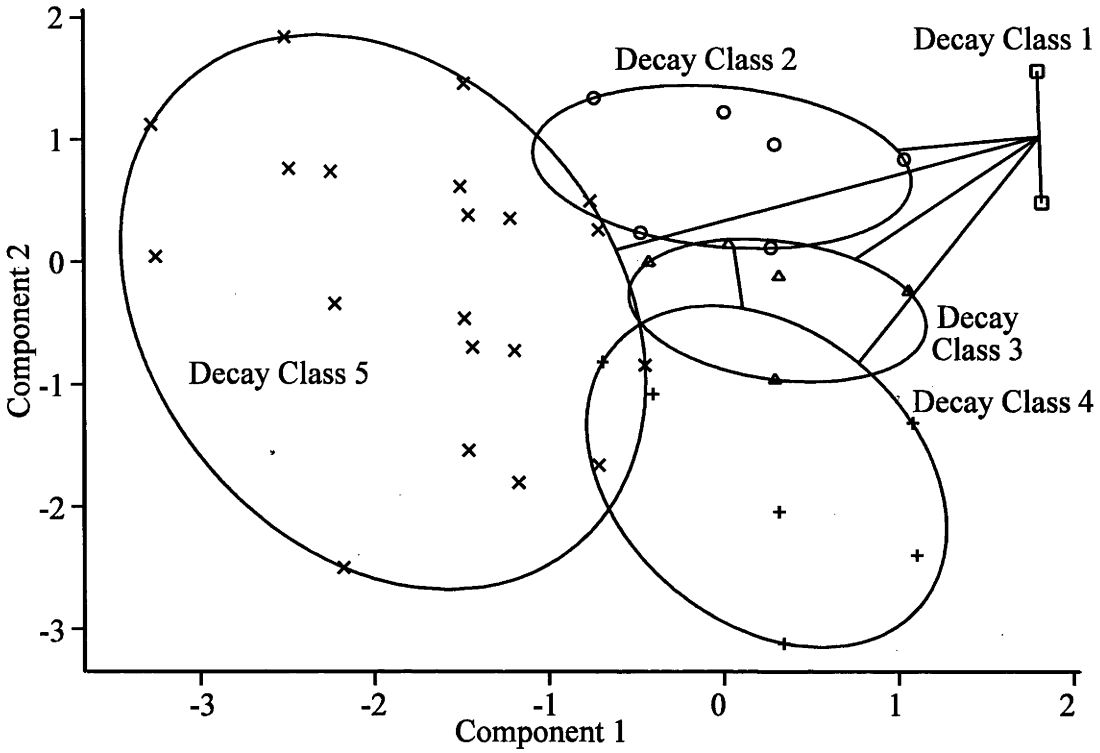
Figure 4-2. Recommended cluster analysis output for central Queensland dry eucalypt woodland samples (*E. crebra* and *E. melanophloia*), showing the five recommended groups of decay classes (n = 93).

4.1.1.4 Far North Queensland

Cluster analyses of the tropical rainforest samples resulted in a five-class system being adopted. The analyses were performed on 133 samples, comprising 74 species. (See Figure 4-3 for the graphical output of the analysis.) Table 4-3 is the five-class decision-tree, used to distinguish between decay classes, for the tropical rainforest of far north Queensland.

Table 4-3. The 5-group decision-tree of decay classification developed from cluster analysis of tropical rainforest CWD samples.

PARAMETER	QUESTION	DECISION	
		YES	NO
Shape	Is the log rubble on the ground?	Class 5	continue
Bark	Is the bark intact (all remaining)?	Class 1	continue
Cracks	Are there deep cracks into the interior of the wood?	Class 4	continue
	Is the log splitting apart?	Class 4	continue
	Are there any surface cracks (not deep) present?	Class 3	Class 2



These two components explain 75.86 % of the point variability

Figure 4-3. Recommended cluster analysis output for mixed species tropical rainforest samples, showing the five recommended groups of decay classes (*n* = 133).

Of interest with the tropical rainforest analysis, is that log density was not useful in distinguishing between the decay classes. This is undoubtedly a result of the enormous breadth of densities of the species when living; some living trees have densities lower than the decaying wood of other species. The 133 samples (74 species) encompassed 53 genera and 28 families.

4.1.2 FREQUENCY DISTRIBUTIONS OF DECAY CLASSES

4.1.2.1 Southern Tasmania

As the samples were collected by the author using a derived decay-class system, and the transects (for CWD field loading) were conducted separately by technicians using a Forestry Tasmania (FT) decay-class system, it was decided to compare the frequency distribution of the two systems (see Figure 4-4). This affords a means of direct comparison between the two systems. As parameter scores were used for the collected samples, and not for the transect surveys, only the 129 collected samples could be used to compare the two systems. The samples were parameter-scored on-site for later determination using cluster analysis, and the classification using the FT system was done *post hoc*, based on the parameter scores. The FT system requires all bark to be remaining on samples for the first decay-class (Class-I), which excluded all samples

collected, as they did not have total bark retention. The lack of bark is undoubtedly due to the intense post-logging slash fires to which the sample-CWD were subjected. (Only samples from logging coupes were collected, as these were the only samples that could be accurately aged.) Consequently, the FT system does not have samples in Class-I; these samples have been absorbed into Classes II-IV. Additionally, no Class-V samples were collected, as the samples of known age (maximum 93 yr) only encompassed wood up to Class-IV.

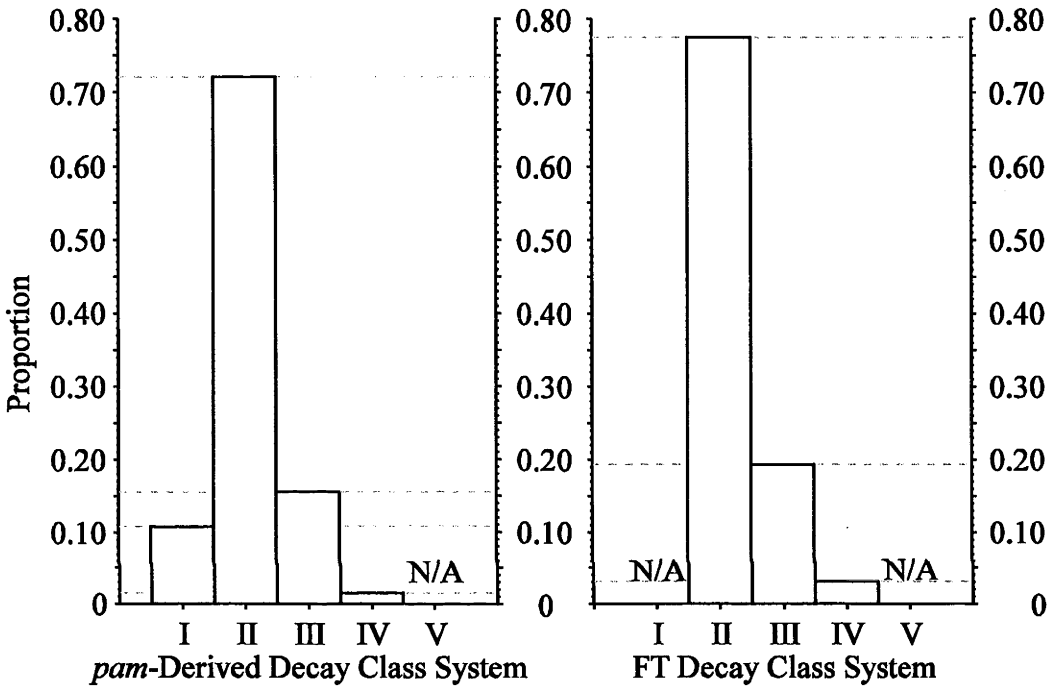


Figure 4-4. Comparison of the decay-class system derived from the *pam* method with the decay class system of Forestry Tasmania (*n* = 129). There is similarity between the two systems, with the exception of the lack of samples in Class-I of the FT system (see text for explanation).

Accounting for the inability to classify collected samples in the first decay-class of the FT system, the frequency distributions are very similar. The frequency-distribution bias toward the lower decay classes is assumed to be due to the 'younger' nature of the samples, as there were no older samples found that could be dated with any sort of accuracy. (All sample-CWD collected was for decay-rate determination, and had to be of known age; see section 4.2 *Decay Rates* for the decay-rate analyses.)

Due to the similarity of the frequency distributions of the *pam*-method and the FT-method, it is assumed that the sample CWD, classified with the *pam*-method, and the transect CWD, classified with the FT-method, can be directly compared to each other (see Figure 4-5).

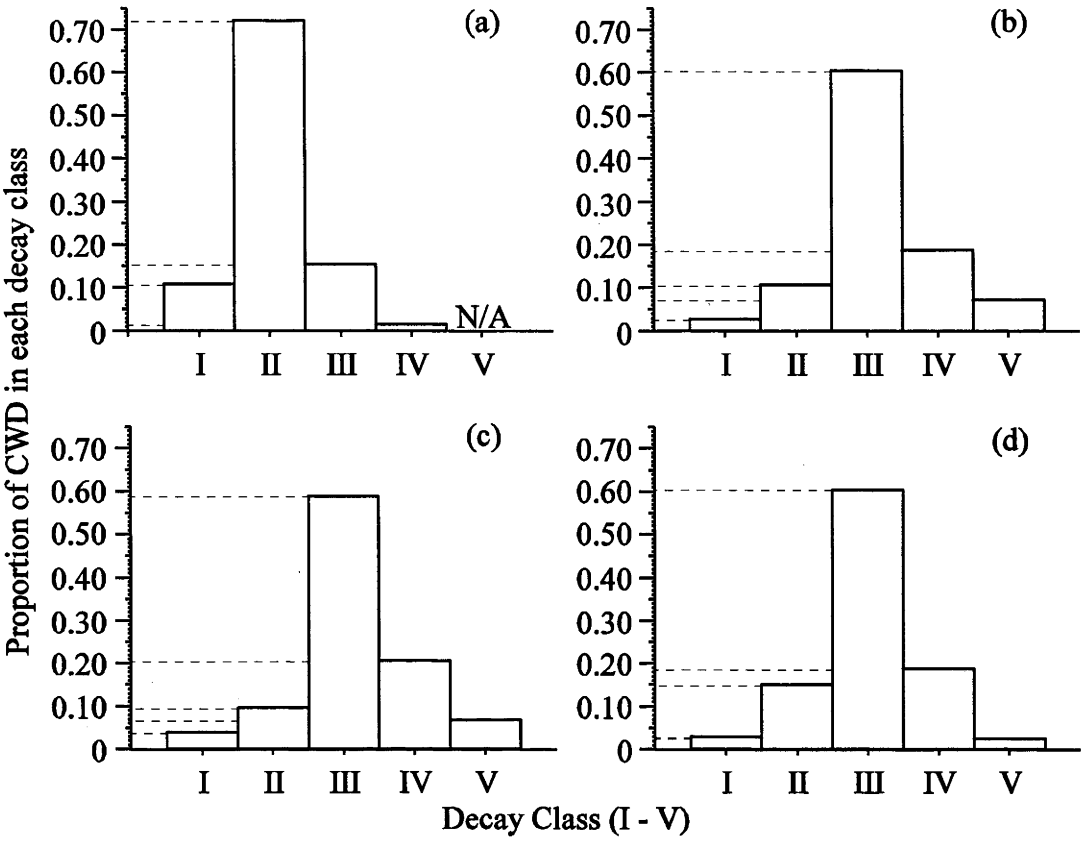


Figure 4-5. Comparison of decay-class frequency distributions of collected *E. obliqua* samples (a; *pam*-method) to transect intersections of different forest types (b-d; FT-method). (a) = samples collected for decay rate analyses (n = 129), (b) = regrowth eucalypt forest with mature trees (n = 578), (c) = mature eucalypt forest without regrowth (n = 2714), and (d) = mature eucalypt forest with regrowth (n = 233).

The comparison of the different decay-class frequency distributions, of the collected samples (from logged coupes) with the different forest types surveyed with transects (Figure 4-5) shows great similarity between the different forest types (Figure 4-5 b-d). The different pattern of the sample CWD (Figure 4-5 a), to the transect CWD, is due to the 'younger' nature of the collected samples (see above). The frequency distribution of decay classes I-IV of the sample CWD is similar to the frequency distributions of classes II-V of the transect CWD. (The sample CWD is assumed to be younger, on average, than the transect CWD, due to the requirement for the sample CWD to be of known age.) It is assumed that the frequency distribution of the sample CWD would shift toward the pattern of the transect CWD as the sample CWD ages further; such a shift would then preserve the pattern of the unimodal near-symmetric distribution pattern, with slightly more samples in the older decay classes than in the younger decay classes.

4.1.2.2 Central Queensland

Both sample and transect CWD was coded *in situ* and later classified into decay classes using the cluster analysis of section 4.1.1.3. The central Queensland decay-class frequency distribution exhibits a bimodal pattern (see Figure 4-6). The entire region has been subjected to gross anthropogenic disturbance, and the pattern may be a reflection of two major clearing events (this is only speculation, as the clearing pattern cannot be confirmed).

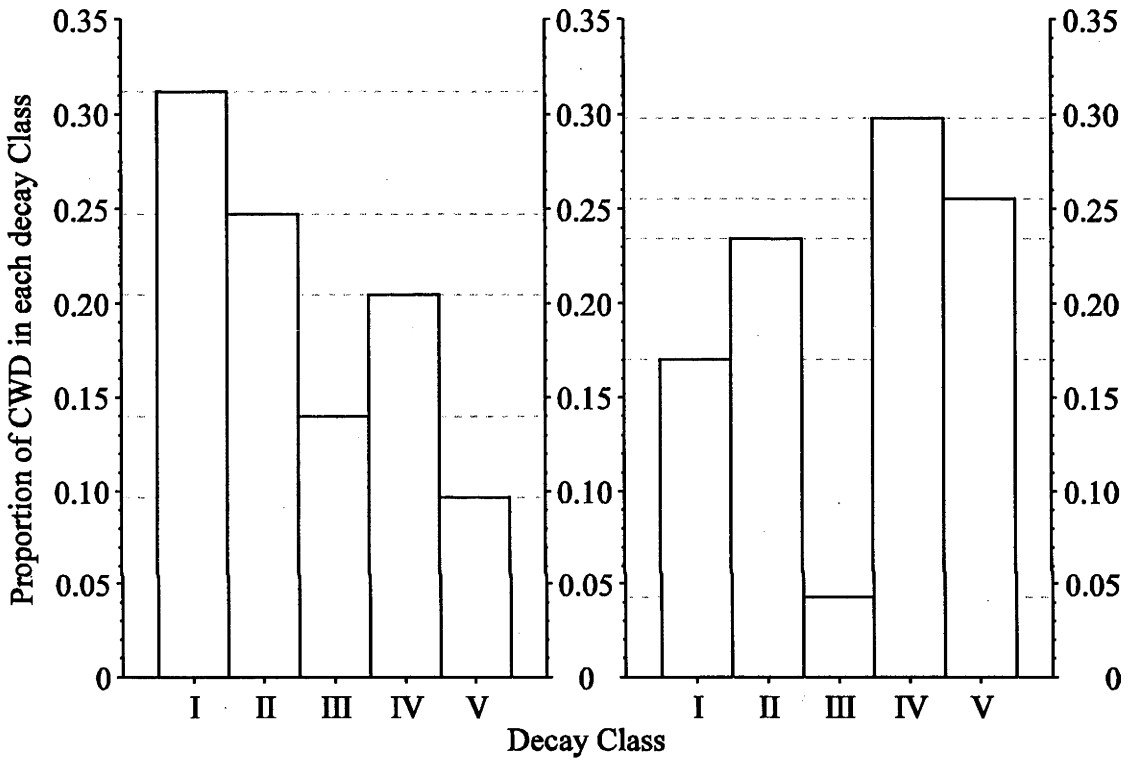


Figure 4-6. Frequency distributions of the collected CWD samples (left, *n* = 93) and the transect-intersected CWD (right, *n* = 47) from the dry eucalypt woodland of central Queensland.

The decreasing pattern of the sample CWD (Figure 4-6) may be a reflection of the samples being younger, on average, than the transect-intersected CWD. The samples collected required that age be known, and, consequently, only included felled trees with archive records, whereas the transect-intersects included samples of all ages, including older CWD than was included in the collected samples. It is assumed that the transect frequency distribution is a more realistic representation of the natural pattern of decay class distribution.

4.1.2.3 Far North Queensland

Both sample and transect CWD were coded *in situ* and later classified into decay classes using the cluster analysis of section 4.1.1.4. The sample and transect CWD frequency distributions are quite similar (Figure 4-7), with a pattern of higher incidence in the latter decay stages. The similarity of the patterns is probably due to the fast decay rate of the CWD in the wet tropical rainforests, resulting in the collected samples (for decay rate determination) encompassing the whole CWD age range existing in the rainforest CWD. (The transect CWD encountered is no older than the CWD collected for samples.)

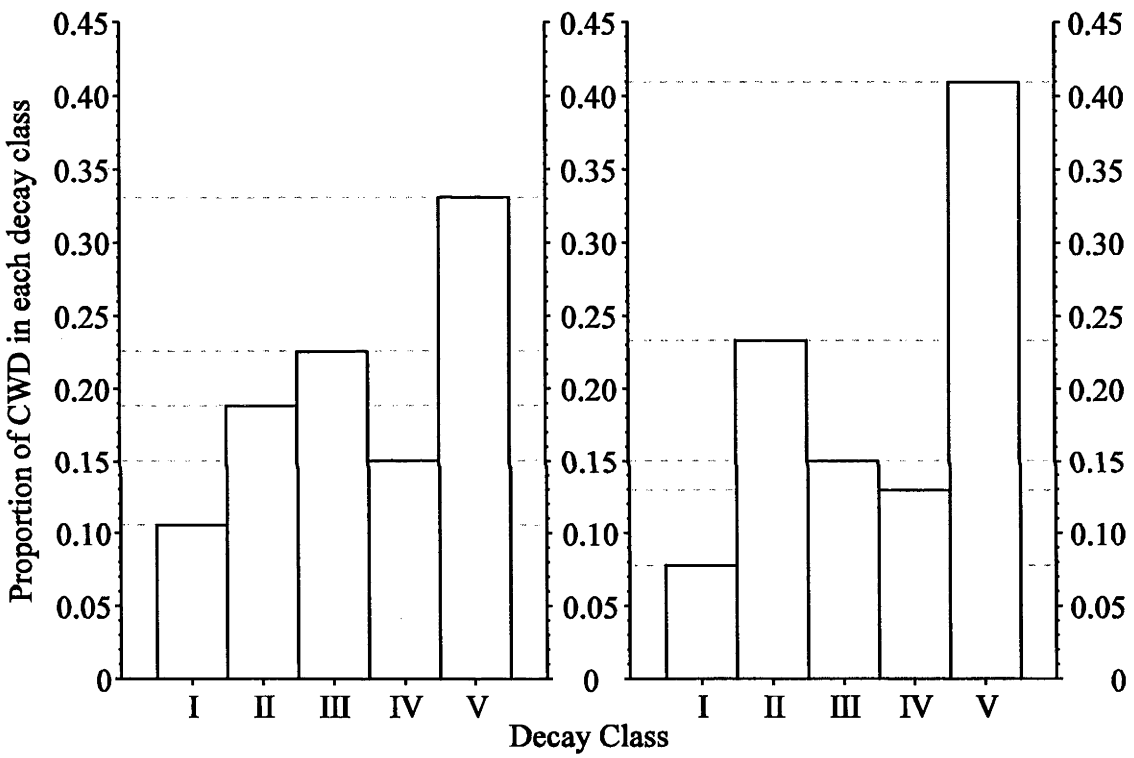


Figure 4-7. Frequency distributions of the collected CWD samples (left, *n* = 133) and the transect-intersected CWD (right, *n* = 193) from the wet tropical rainforest of far north Queensland.

4.1.2.4 Comparison of Decay Class Distributions

The comparison of CWD frequency distributions (Figure 4-8) was done using only transect CWD as it encompassed the full range of CWD ages found in the environments studied. The southern Tasmanian transect-CWD was classified using the Forestry Tasmania decay class system and the central and far north Queensland transect-CWD was classified using the systems derived from cluster analyses (see section 4.1.1 *Determination of Decay Classes*). However, the frequency distribution of the FT

system was shown to be comparable to the system derived from the cluster analyses, as used for the Queensland frequency distributions (see section 4.1.2.1 *Southern Tasmania*; *Frequency Distributions of Decay Classes*), consequently, the transect frequency distributions are deemed to be directly comparable.

The immediate difference between the decay-class frequency distributions is the very peaked nature of the wet eucalypt forest CWD of southern Tasmania compared to the dry eucalypt woodland CWD of central Queensland and the wet tropical rainforest CWD of far north Queensland. Both the central Queensland CWD and the far north Queensland CWD have the majority of the CWD in the final two decay stages (IV and V), whereas less than a quarter of the southern Tasmanian CWD is in the final two decay stages.

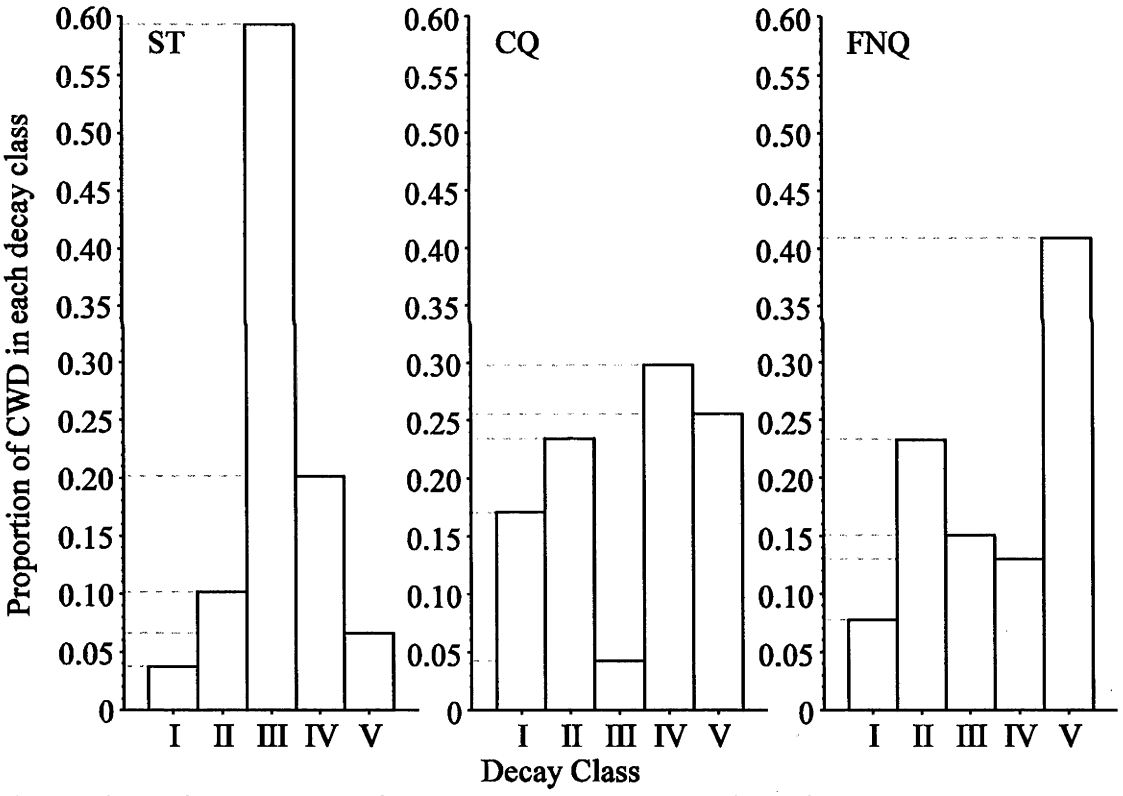


Figure 4-8. Comparison of transect CWD distributions for southern Tasmania (ST; *n* = 3525), central Queensland (CQ; *n* =47), and far north Queensland (FNQ; *n* = 193).

4.1.3 DECAY CLASS VS. CWD AGE

Collected CWD samples were analysed by plotting decay class against CWD age, but there was no correlation between the two variables. This lack of correlation is undoubtedly due to the influence of other factors, such as microclimate, relative

proportions of nutrients and toxins between the different species (only the southern Tasmanian sampling consisted of a single species), and the decomposer organisms present in the relevant ecosystem. A multiple regression analysis of the decay rates versus physical site characteristics is performed in section 4.4 *Multiple Regression Analyses*.

4.2 DECAY RATES

The single-exponential model (SEM) was used to fit decay-curves to the data (see section 3.2 *Decomposition Models for CWD*). Relative density (density of sample as a proportion of green density) was used as the response variable, with age the predictor variable. The regional climate and ecosystem type, for the samples used in the determination of the decay rates, are shown in Table 4-4.

Table 4-4. Forest types and prevailing climates of regions studied.

Region	Forest Type	Climate
FNQ = Far North Queensland	**Wet tropical rainforest**	**Tropical**
NSW = South Coast NSW	**Wet eucalypt forest**	**Temperate**
ST = Southern Tasmania	**Wet eucalypt forest**	**Cool Temperate**
CQ = Central Queensland	**Dry eucalypt woodland**	**Subtropical**

Although these were 111 samples available for the southern Tasmanian decay-rate analysis, 12 of these were excluded from the analyses due to disproportionately high influence upon the regression analysis. These samples were all over 45 cm in diameter; with a diameter range from 62-188 cm (see Figure 4-9). There was a significant difference ($p < 0.0001$) between the <45 cm samples and the >45 cm samples. Analysis of both subgroups (<45 cm & >45 cm diameter) and the whole sample set (all 111 samples combined) showed a significant difference ($p < 0.0001$) between all three groups. Consequently, all 12 samples >45 cm in diameter were removed from the analyses due to their disproportionately high influence upon the regression analyses.

Change in density as a function of time was used to determine the decay rates of the CWD samples collected; using the SEM. The idea behind this method is that density will decrease over time, as the wood decays. However, while this trend was observed in

the CWD samples collected from the wet forests, the central Queensland samples exhibited an increase in density over time (see Figure 4-10). The central Queensland data was treated as a special case, and were excluded from the exponential decay-model analyses. The reason for the increasing density of the central Queensland samples is due to the affect of extreme microclimate, and is covered further in the Discussion Chapter.

All SEM curves for the wet forests studied, despite the wet eucalypt forests having low *k*-values, were significantly different from a horizontal line (no decay); see *p*-values of Table 4-5. Of the wet forests, the tropical rainforest was significantly different from the wet eucalypt forests ($p < 0.0001$). The overall *k*-value for the tropical rainforest was 0.1121 yr^{-1} ($p < 0.0001$; model curve is significantly different from zero) and was 0.006618 yr^{-1} ($p < 0.0001$) for the wet eucalypt forests. Due to the different pattern of density-change over time for the central Queensland samples, it is obvious that the central Queensland samples are decaying in a significantly different pattern than the samples from the wet forests (despite no direct statistical comparisons being possible).

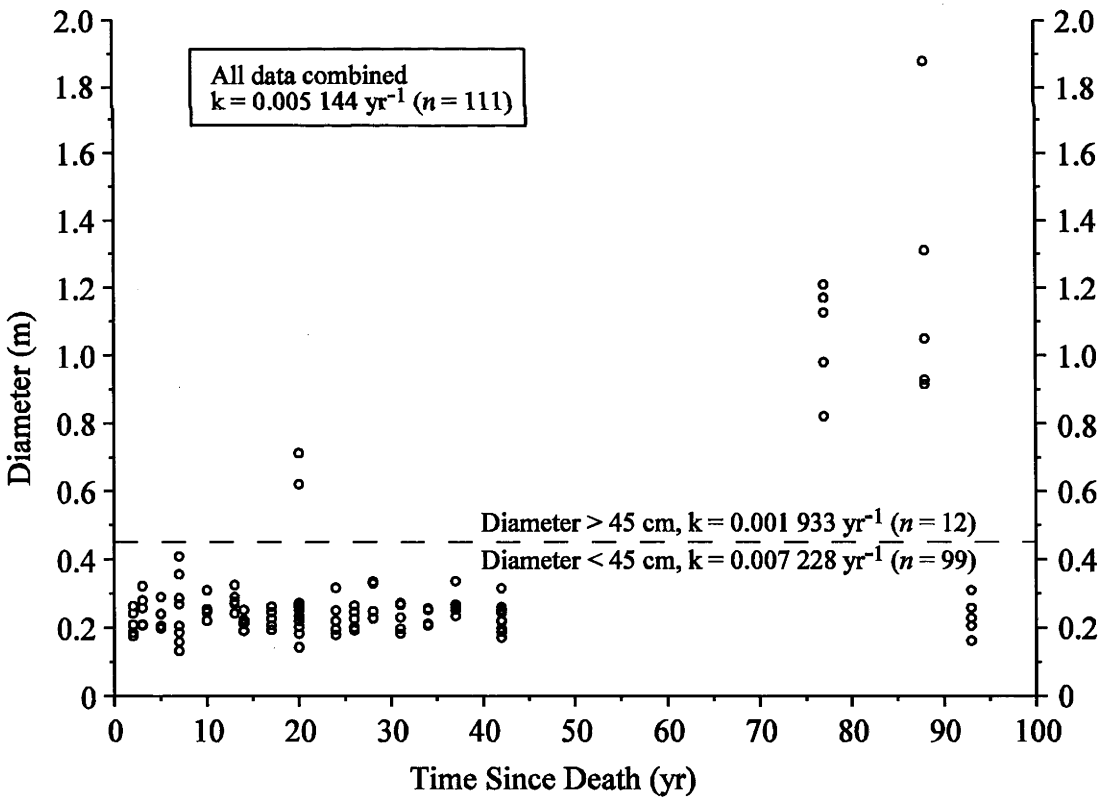


Figure 4-9. Diameter distribution of southern Tasmanian CWD samples.

The analyses of the wet eucalypt forests was done with the NSW sites segregated into the area that was included into Murramarang National Park and the sites remaining

in Benandarah State Forest, and the Tasmanian sites were segregated by the compartmentalisation used by Forestry Tasmania (see Table 4-6). These segregation locations are arbitrary, and do not reflect any definitive stratification. Due to regional homogeneity, the only difference within a region is the geographical difference, although all locations within a region were adjoined. The only discernible heterogeneity was between the regions, which are approximately 900 km apart.

Analysis of the *k*-values for the Tasmanian and NSW wet eucalypt forests showed no significant differences between the regions (p = 0.1585). Analysis of the locations within each region (see Table 4-6) showed that there were no significant differences for the Tasmanian (p = 0.2724) and NSW (p = 0.9437) samples. Analysis of all six locations combined, from both regions, showed no significant differences (p = 0.3142), despite the geographical separation, and different resident eucalypt species.

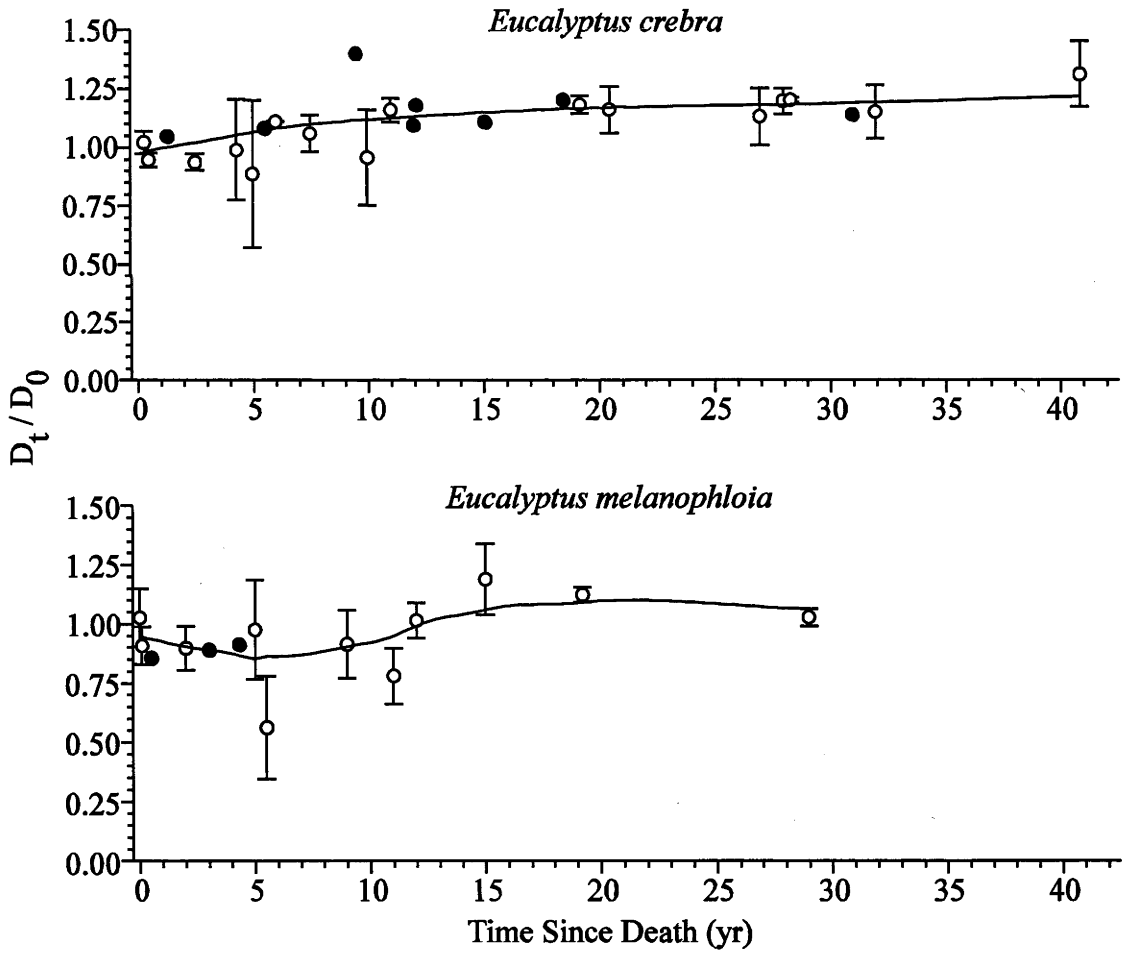


Figure 4-10. Central Queensland CWD sample densities, sorted by species. Error-bars are standard error, ○ are the mean values, and • are single samples. The fitted-line is a loess (local regression) fit. Note how density increases with time.

Note that the Tasmanian CWD samples, of Figure 4-11, show an 'outlier-group' of samples (n = 5) that are aged 93 years old and the next oldest group is 43 years old. Decay-rate-analyses were run with-and-without these older-samples to test for the affect of these older samples for possible disproportionately high-influence upon the regression analyses. The single-exponential model (SEM) k-value (decay model constant) was 0.007228 yr^{-1} with these older-samples included, and 0.007020 yr^{-1} with the older-samples excluded. A comparison of the fitted SEM k-values showed these fitted curves to not be significantly different (p = 0.8892). Consequently, it was decided that the decay-rate analyses of the Tasmanian CWD include the 93-year-old samples, and the accepted k-value for the Tasmanian CWD was 0.007228 yr^{-1} (see Table 4-5).

Table 4-5. Single-exponential model (SEM) output for the studied regions. RSS = residual sum of squares. See Table 4-4 for a description of the region codes. The central Queensland data could not be analysed with the SEM. Note, p-values shown are testing whether the k-values are significantly different from zero (a horizontal line).

Region	Forest Type	n	k-value (yr^{-1})	$t_{0.95}$ (yr)	Standard Error	p-value	RSS
FNQ	Wet tropical rainforest	40	0.1121	26.73	0.01134	< 0.0001	1.676
NSW	Wet eucalypt forest	48	0.005538	540.9	0.0008054	< 0.0001	0.8533
ST	Wet eucalypt forest	99	0.007228	414.5	0.0007820	< 0.0001	2.704
CQ	Dry eucalypt woodland	-	-	-	-	-	-

Table 4-6. Names of locations within the wet eucalypt forests of the two regions sampled.

Forest Region	Location (sites within region)	Species
NSW South Coast	Benandarah State Forest	Mixed *Eucalyptus*
NSW South Coast	Murramarang National Park	Mixed *Eucalyptus*
Southern Tasmania	Arve District	*E. obliqua*
Southern Tasmania	Geeveston District	*E. obliqua*
Southern Tasmania	Picton District	*E. obliqua*
Southern Tasmania	Warra District	*E. obliqua*

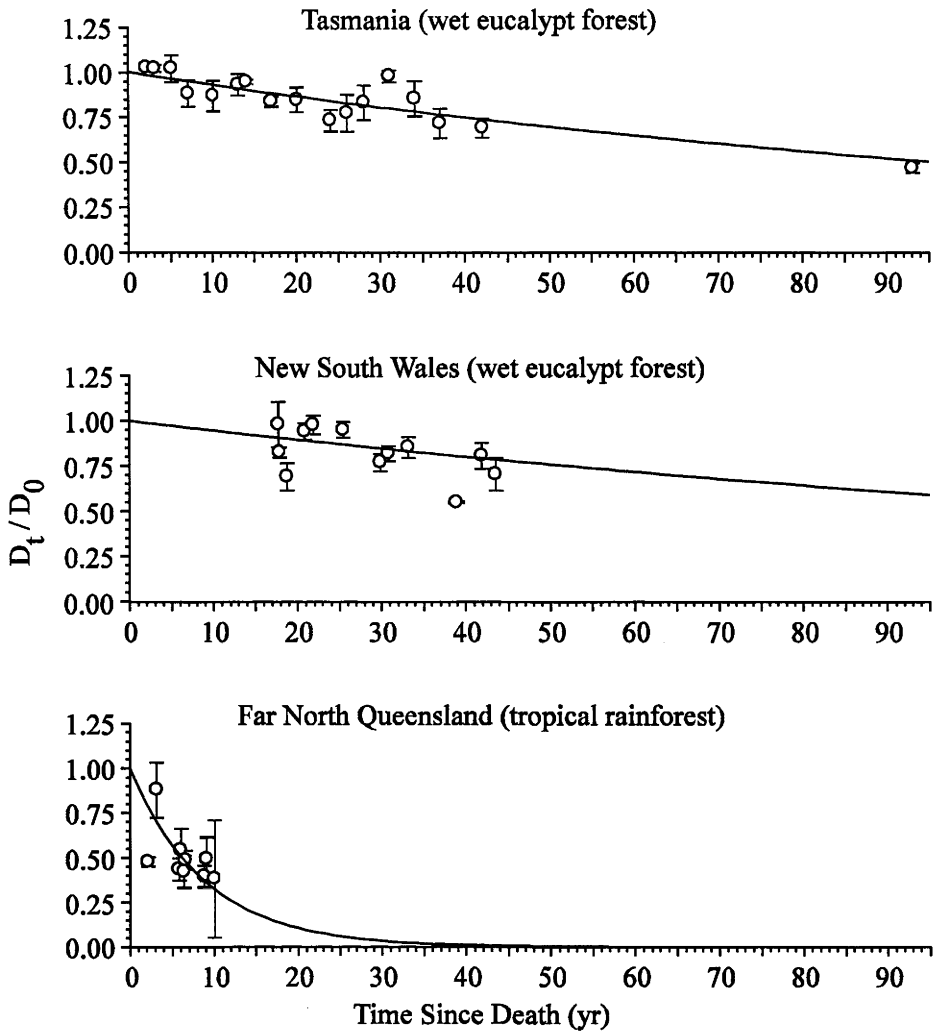


Figure 4-11. Wet forest CWD sample densities, sorted by region, showing mean values with standard error bars. See Table 4-5 for the *k*-values of the fitted single-exponential models.

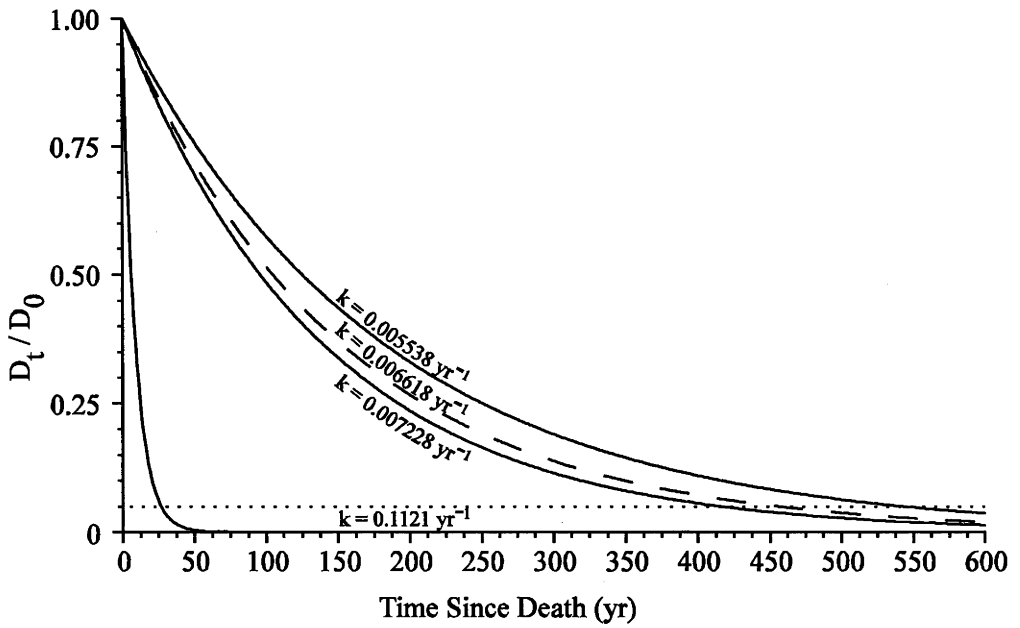


Figure 4-12. Single-exponential model decay curves for (top to bottom) NSW south coast, southern Tasmania, and far north Queensland. Dashed line is the overall decay curve for the wet eucalypt forests of NSW and Tasmania. Dotted line is 5% of initial density remaining (corresponds to $t_{0.95}$).

Shown in Figure 4-12 are the single-exponential model curves from the non-linear least squares regression. Of interest is that the marked difference of the curves for the wet eucalypt forests and the wet tropical rainforest.

4.3 AMOUNT OF CWD IN THE ENVIRONMENT

This section is dealing with the actual amount of wood measured in the environments studied during fieldwork. The terms 'environmental volume' and 'environmental mass' are used to signify the actual amount of CWD volume or mass measured in the field surveys. The term 'environmental' is used to distinguish the amount of CWD wood from sample volume and sample mass as measured in the laboratory during sample processing. (The use of the term 'environmental' is used to explicitly state that the measurements/calculations refer to the CWD in the environment; that is, this section is dealing with environmental volume (m^3 ha^{-1}) and environmental mass (Mg ha^{-1}), and is not dealing with sample volume (cm^3) and sample mass (g).)

4.3.1 CWD ENVIRONMENTAL VOLUMES

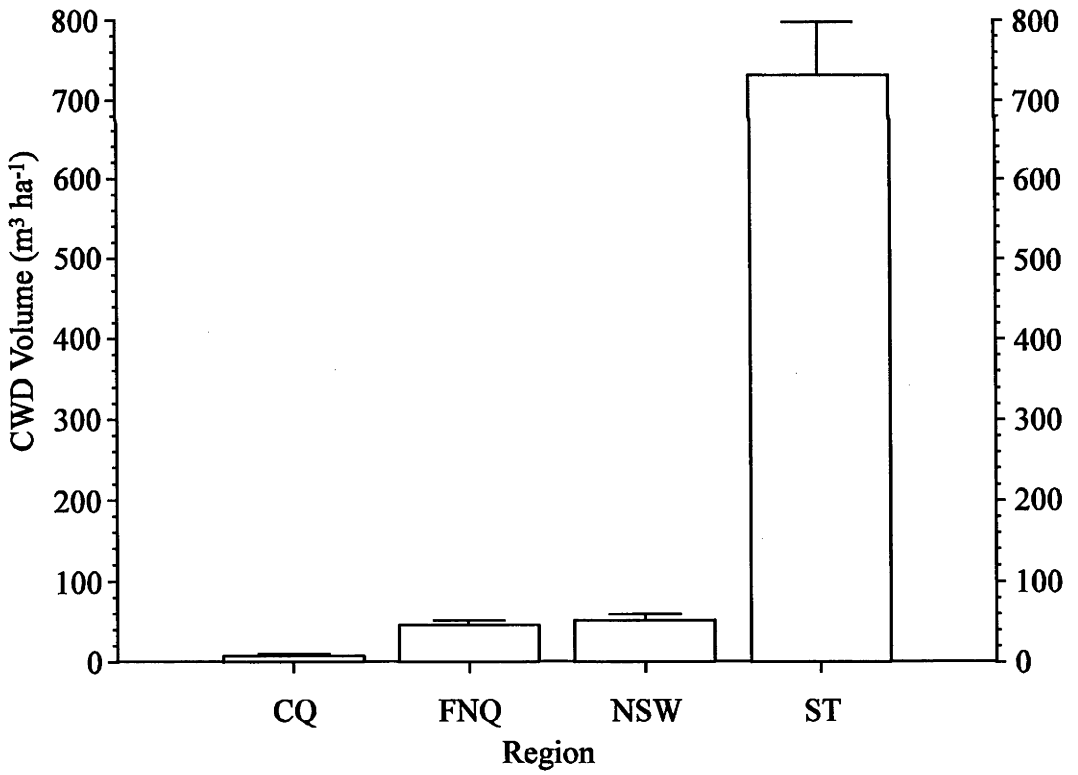


Figure 4-13. Volumes of CWD for the dry eucalypt woodland of central Queensland, the wet tropical rainforest of far north Queensland, the wet eucalypt forests of the New South Wales south coast and southern Tasmania. Bars are standard errors.

The environmental volume (m^3 ha^{-1}) of CWD (Figure 4-13) shows an extraordinarily high volume loading for the CWD of southern Tasmania (ST), compared to the other regions. The CWD loading of central Queensland (CQ) is low due to the low tree-density (trees ha^{-1}) of the woodland landscape, and the low tree height compared to the forest regions. The tropical rainforest of far north Queensland (FNQ), despite having a high tree-density, has a relatively low CWD loading due to its very high decay rate (see section 4.2 *Decay Rates*) resulting in greatly shortened residence time for individual CWD pieces. The CWD from the New South Wales south coast sites (NSW), despite having similar decay dynamics to the Tasmanian CWD, has a low CWD loading due to all areas being subjected to anthropogenic disturbance, and the actions of wood collecting from a larger surrounding-human-population. Conversely, some Tasmanian transect sites were in undisturbed forest.

4.3.2 CWD ENVIRONMENTAL MASS

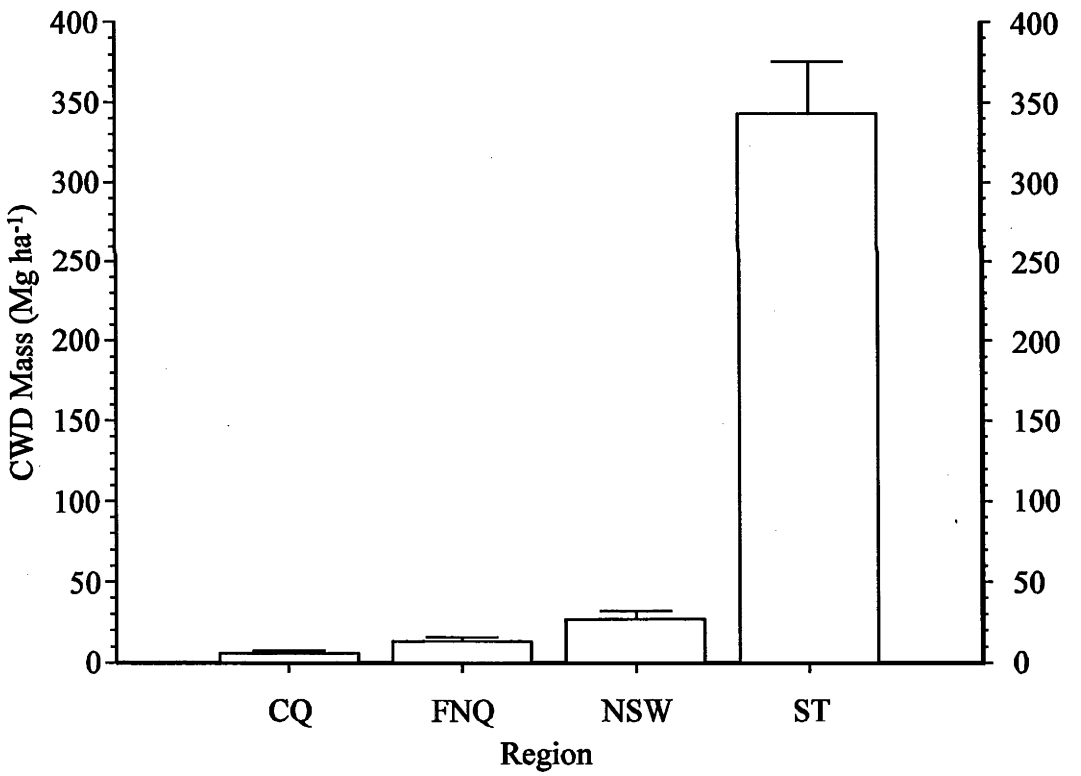


Figure 4-14. Environmental mass of CWD, bars are standard errors. CQ = central Queensland, FNQ = far north Queensland, NSW = New South Wales south coast, and ST = southern Tasmania.

The higher CWD volume loading of the southern Tasmanian CWD is also reflected in the environmental mass loading (Mg ha^{-1}) of the CWD (Figure 4-14). (See section 3.5.1 *Collection and Storage of Samples Prior to Analyses* for a description of the

calculation of the environmental mass.) Although the volumes for FNQ and NSW were similar, the FNQ mass loading is only about half that of NSW, due to the mean density of the FNQ samples being only about half that of the NSW samples. The CQ mass loading is the lowest of all, due to the low tree-density of the woodland, and the history of intense anthropogenic disturbance.

4.3.3 CWD ENVIRONMENTAL CARBON RELEASE

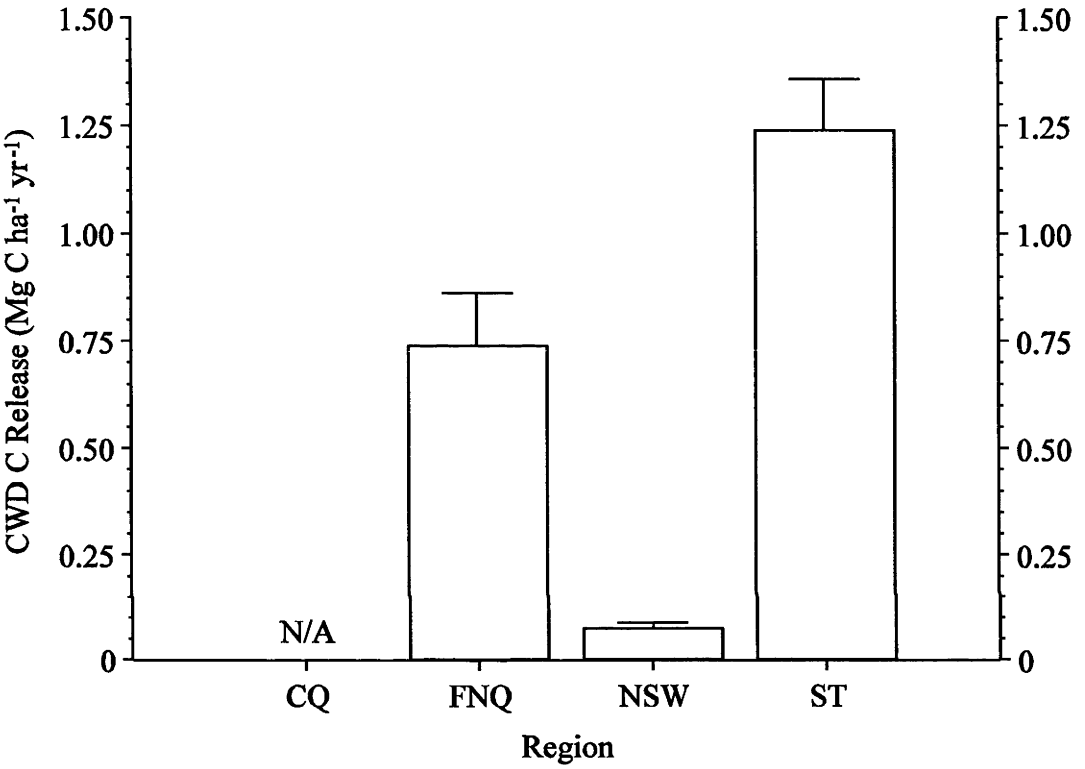


Figure 4-15. Carbon release from CWD of far north Queensland, New South Wales south coast, and southern Tasmania; central Queensland is not shown as there is no single-exponential model constant (*k*-value) available for CWD decay of central Queensland. Bars are standard errors. The graph is showing actual carbon (C) release to the environment, not carbon dioxide (CO_2) release.

Carbon release/loss (Figure 4-15) was calculated as the mass of C released to the surrounding environment (Mg C ha^{-1} yr^{-1}), and not the amount of CO_2 released. This calculation is necessary as some of the carbon is incorporated into the mass of the decomposer organisms utilising the CWD. Carbon release calculations were done assuming the C mass content to be 50% of the wood mass; this allows comparability with many researchers (e.g., Foster and Lang 1982; Mattson *et al.* 1987: Schowalter 1992; Karjalainen 1996; Schowalter *et al.* 1998; Mackensen and Bauhus 1999; Chambers *et al.* 2000; Robertson et al. 2000; Woldendorp 2000; Chojnacky and Heath

2002; Mackensen *et al.* 2003). Due to the inability to model the CQ data with the single-exponential model (SEM), there was no possibility of calculating carbon release or retention (see section 4.3.4 *CWD Environmental Carbon Retention*) for CQ.

Despite the low decay rate of the wet eucalypt forest CWD of southern Tasmania (ST), the C release is still high due to the very high volume and mass loadings of the ST CWD. In comparison, the wet eucalypt forest CWD of NSW, despite having a comparable decay rate to the ST CWD, has a much lower C release rate due to the much lower CWD loadings for NSW. The wet tropical rainforest CWD of FNQ, despite having low CWD loadings compared to ST, has a high C release rate due to the high decay rate of the CWD.

4.3.4 CWD ENVIRONMENTAL CARBON RETENTION

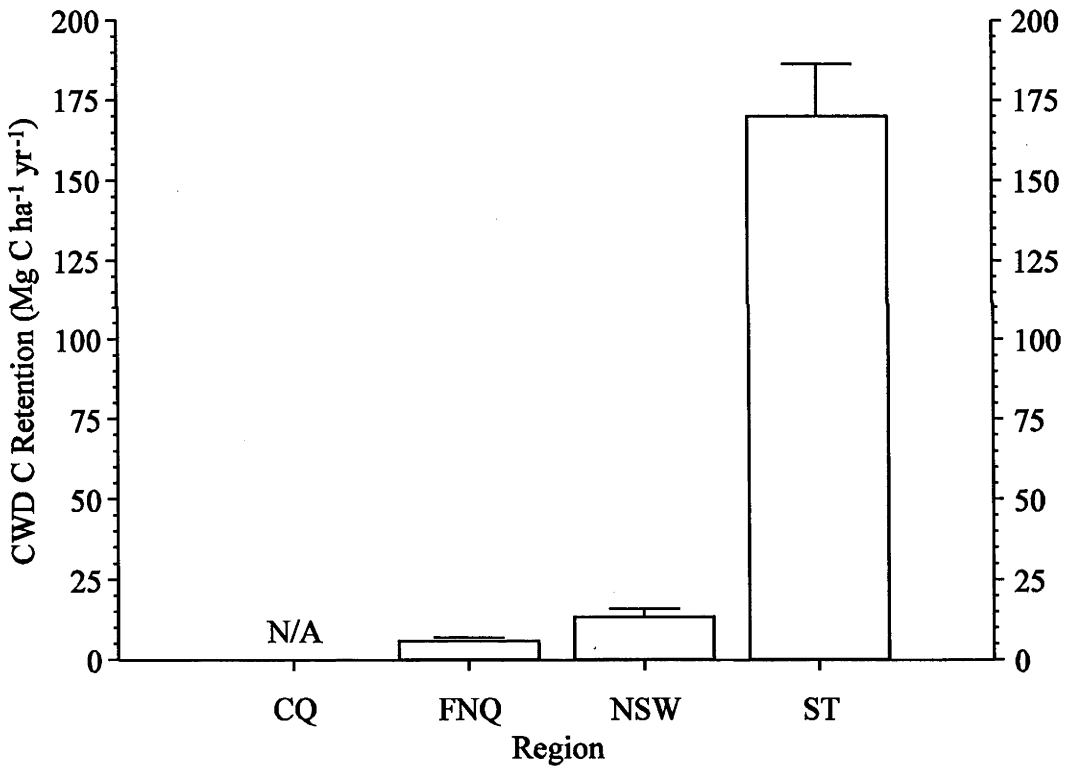


Figure 4-16. Carbon retention by CWD, the amount of C not being released each year, for the rainforest of far north Queensland, and the eucalypt forests of New South Wales south coast and southern Tasmania; central Queensland is not shown as there is no single-exponential model constant (*k*-value) available for CWD decay of central Queensland. Bars are standard errors.

It was decided to calculate C retention as a means of putting the C release into context, as high C release from an individual site is not necessarily a symptom of undesirable CWD decay; as it may be an artefact of high mass loadings with low decay

rates. Carbon retention is the amount of C not released to the surrounding environment over any given time period, but, rather, remains sequestered within the CWD of that environment. Carbon retention (Figure 4-16) was calculated as the mass of C retained by the CWD of each region, and not the amount of CO_2 retained. (See previous section for justification.) Carbon retention of the CQ CWD could not be calculated for the same reason given in the previous section.

The C retention of the southern Tasmanian CWD is very large at 170.2 Mg ha^{-1} yr^{-1} (SE = ± 16.00 mg ha^{-1} yr^{-1}), compared to the 1.239 Mg ha^{-1} yr^{-1} (SE = ± 0.1165 Mg ha^{-1} yr^{-1}) C release, which shows that the large C release is caused by a slow decay rate coupled with a high environmental CWD mass loading. However, the relatively low C retention of the FNQ tropical rainforest CWD shows that the high C release is the result of a fast decay rate. The low C retention of the NSW CWD is due to the low environmental mass of the CWD, as also evident by the low C release.

4.3.5 CWD ENVIRONMENTAL AMOUNTS BY DECAY CLASS

As the southern Tasmanian sample CWD only encompassed decay-classes I-IV, the ST CWD amounts, by decay class, can only be determined for these classes.

The New South Wales sample and transect CWD was not coded for decay class determination (see section 3.3.2 *Decay Classes*; Methods Chapter), therefore, there are no data to construct decay-class distributions for the CWD amounts for NSW.

4.3.5.1 Southern Tasmanian CWD Amounts and Carbon Flux by Decay Class

The CWD amounts for each decay class, for the wet eucalypt forest of southern Tasmania (Figure 4-17), only include decay-classes II-IV, due to different classification systems being used for the collected samples and the transect sampling. As the sample CWD, whose densities are required for mass calculations, could only be classified into decay-classes II-IV of the Forestry Tasmania system, only these decay classes could be used for the CWD environmental amounts. (See section 4.1.2 *Frequency Distributions of Decay Classes* for a thorough explanation, and a description of the comparison method.)

The pattern of the CWD amounts closely resembles the frequency distribution pattern of the transect-intersected CWD (graphs (a)-(d) of Figure 4-17), with the pattern of Class-II < Class-IV < Class-III. Decay-class III typically accounts for about ⅔ of the CWD amounts represented by the three decay-classes.

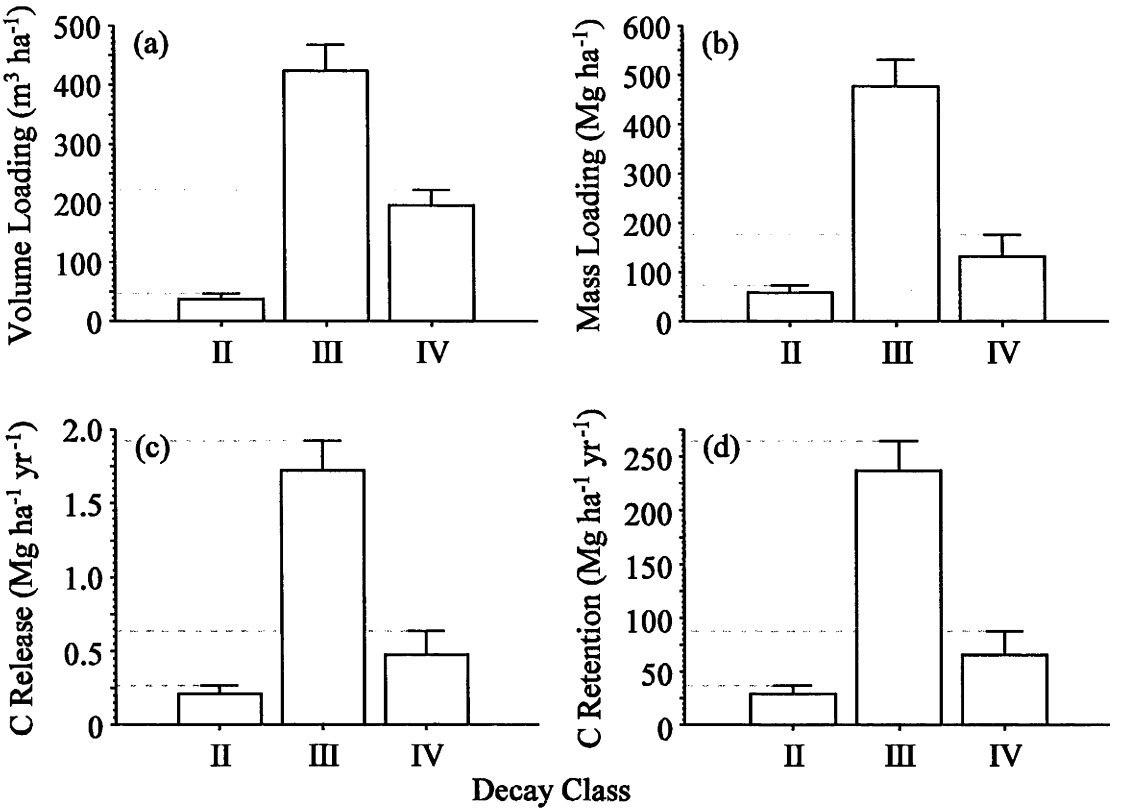


Figure 4-17. Coarse woody debris amounts for the wet eucalypt forest of southern Tasmania. Bars are standard errors.

4.3.5.2 Central Queensland CWD Amounts by Decay Class

As the central Queensland CWD could not be modelled with the single-exponential model (see section 4.2 *Decay Rates*), the C release and retention values could not be calculated, and, as such, do not appear in Figure 4-18. Consequently, this section only shows the CWD volume and mass loadings, by decay class.

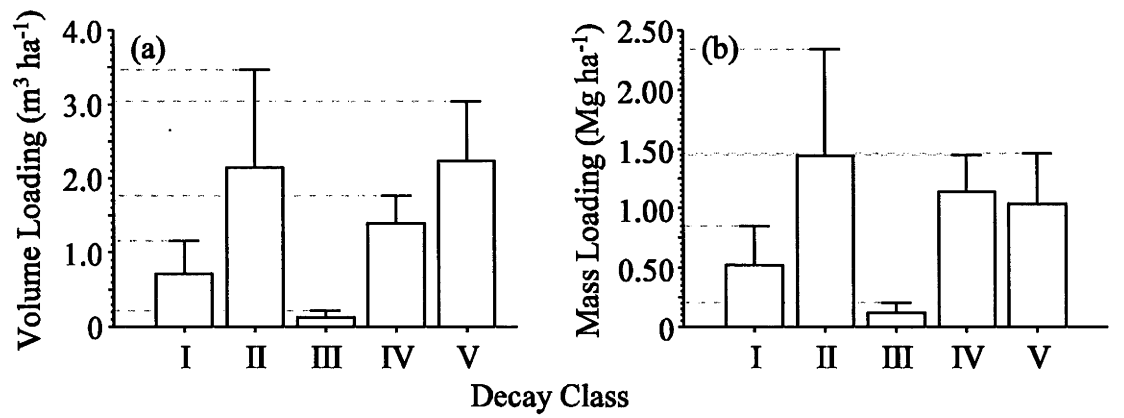


Figure 4-18. Coarse woody debris amounts for the dry eucalypt woodland of central Queensland. Bars are standard errors.

The pattern of the volume and mass loading, by decay class, is similar to the transect-CWD frequency distribution of Figure 4-6. Where the pattern of the southern Tasmanian CWD environmental amounts (Figure 4-17) appears uni-modal, the central Queensland CWD environmental amounts appear to be bi-modal. A possible explanation for the bi-modal pattern is given in section 4.1.2.

4.3.5.3 *Far North Queensland CWD Amounts and Carbon Flux by Decay Class*

The environmental volumes, mass, C release, and C retention, by decay class, of the wet tropical rainforest CWD of far north Queensland (Figure 4-19) exhibits a similar pattern to the frequency distributions of Figure 4-7. The CWD amounts are very low, due to the fast decay rate resulting in a short residency-time for the CWD. The first four decay classes of Figure 4-19 show a general uni-modal pattern, however, decay-class V appears as a spike with the highest values of all the classes. This suggests that a pulse of CWD has occurred in the past, with a resultant over-representation of Class-V CWD. This increased CWD formation in the past, may also explain the 'drop-off' in Class-IV CWD, as unhealthy trees may have been removed *en masse* in the pulse-event, resulting in lower numbers of tree deaths during the period of Class-IV CWD.

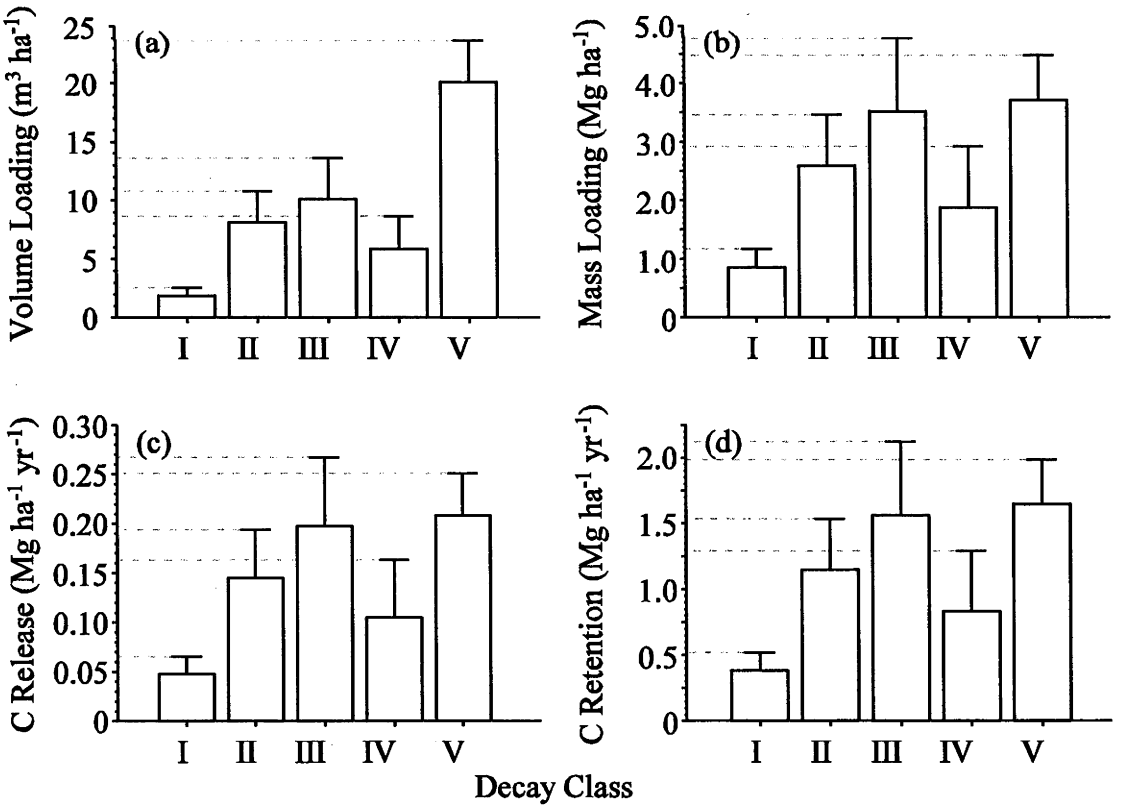


Figure 4-19. Coarse woody debris amounts for the wet tropical rainforest of far north Queensland. Bars are standard errors.

Tropical cyclones may account for some of the CWD input-pulse, but as the regional coverage is large, it is unlikely that cyclones can be any more than a minor contributing factor to the pulse. Dieback (*Phytophthora cinnamomi* Rands) is a recurring phenomenon in the rainforest, but infection varies both spatially and temporally, which also relegates dieback to a minor role in the CWD input-pulse. The pattern show warrants further investigation of causes of tree mortality in the rainforest.

4.4 MULTIPLE REGRESSION ANALYSES

Multiple regression analyses (MRA) were performed using the proportional remaining density as the response variable; this is the sample density divided by the 'green' density of the living tree (from the literature). The predictor variables used in the analyses were: time since death (age as CWD), the diameter of the CWD sample (calculated as the geometric mean of the horizontal and vertical diameters), latitude, longitude, altitude, slope of sample collection site, aspect of site, mean annual temperature, and mean annual rainfall. The difference in the directional angle of the CWD piece and the aspect (Δ-angle) was also assessed for all regions except for the NSW sites; as the decision to collect this data was not made until after the NSW sampling was completed. Proportional canopy cover was also assessed as a predictor variable, but was not available for the NSW sampling.

The decision to include or exclude parameters (individual variables and interaction terms) was based on the Akaike Information Criterion (AIC). The initial model reduction was performed using stepwise analyses using the *stepAIC* function; available from the MASS library of Venables and Ripley (2000), which is available with S-PLUS. The *stepAIC* command of the MASS library is considered superior to the standard S-PLUS *step* command (Venables and Ripley 2000, Millard and Neerchal 2001). Backwards and forwards stepwise regression was used to provide recommended predictor variables for the main analyses.

The main analyses was performed using the standard linear-model command (S-PLUS command *lm*), and assessing each parameter by the *F*-statistic. When possible, Type-III ANOVA was used to assess individual *F*-statistic *p*-values, as Type-III ANOVA is not order dependent. However, there were occasions when Type-III ANOVA was invalid, usually due to the interaction terms, and Type-I ANOVA was used. Type-I ANOVA is order dependent, with only the last parameter on the model-string able to be assessed by its *F*-statistic *p*-value, and this often required

changing the order of the parameters in the model. An α-value of 0.05 was used to determine significance.

4.4.1 SOUTHERN TASMANIA

The initial analyses included all data combined (n = 111, all *E. obliqua*), and showed Time Since Death ($p < 0.0001$), Diameter ($p<0.0001$), and Mean Annual Temperature ($p = 0.0499$), as significant factors in the CWD decomposition at this location (consisting of wet eucalypt forest).

4.4.2 NEW SOUTH WALES SOUTH COAST

Only a relatively small number of samples (n = 48, mixed *Eucalyptus* species) could be accurately dated at the NSW sites (wet eucalypt forest sites). The MRA showed that Time Since Death ($p = 0.0189$), Altitude ($p < 0.0001$), and Slope ($p = 0.0015$), were significant in the decomposition of CWD at this location.

4.4.3 WET EUCALYPT FORESTS

The wet eucalypt forest data of southern Tasmania and the NSW South Coast were combined, to test the sites from the two separate regions together (n = 159, mixed eucalypt species). As for the NSW data, Δ-angle and canopy cover were not available for the analyses; due to the data not being collected for the NSW samples.

Analyses showed that Time Since Death ($p < 0.0001$), Diameter ($p < 0.0001$), and Rainfall ($p = 0.0258$), were significantly correlated with change in specific density.

4.4.4 CENTRAL QUEENSLAND

The central Queensland analyses (n = 88, *E. crebra* and *E. melanophloia*) showed that Time Since Death ($p < 0.0001$) and Species ($p = 0.0026$) were significantly correlated with change in specific density.

However, the specific density did not show evidence of decrease over time (from the samples collected), and the correlation shown cannot be classified as evidence of determining factors in the decomposition of the CWD at the sites in the central Queensland region studied. (See section 4.2 *Decay Rates* for further explanation regarding the failure of specific density to decrease over time.)

4.4.5 FAR NORTH QUEENSLAND

The analyses of the tropical rainforest sites ($n = 41$, mixed species) showed that Time Since Death ($p = 0.0151$) was the only predictor variable studied that was significantly correlated with the change in specific density.

4.4.6 TREE-MODEL ANALYSES

Due to the multiple regression analyses being performed over the entire range of the response (relative density) and predictor variables, it was decided that stratification of the datasets might provide further insight into the significance of the predictor variables at different stages of the decomposition process.

It was decided that stratification could be achieved by the use of tree modelling, using the standard S-PLUS function *tree*; this method produces a tree-diagram with dichotomous splitting. The tree model method produces a tree-diagram with splits producing groups with a predetermined minimum number of samples included. It was decided that the default minimum number of $n = 5$ would be used for the tree-models.

The tree-model was checked for agreement with the MRA at all nodes along a single path, using the tree-model for the southern Tasmanian data. All splitting-nodes (intermediate-nodes) and the terminal-node ('leaf-node') were checked for agreement with the MRA. Unfortunately, there was no agreement between the parameters recommended by the tree-model method and the MRA method. The lack of agreement is probably due to the different methods of determining which parameters represent the change in specific-density. The MRA uses the F-statistic to determine significance of correlation, whereas the tree-model method determines a split based on which value of which predictor-variable will result in the best dichotomous split of the data, at each particular node.

4.4.7 SUMMARY OF MULTIPLE REGRESSION ANALYSES

Table 4-7 is a summary of the multiple regression analyses for the studied sites, where predictor-variables and interactions were assessed against change in specific density.

Table 4-7. List of significant predictor-variables as tested against change in specific density of samples collected at sites from four regions in eastern Australia. Interaction terms were analysed, but none were significant. (TSD = Time Since Death; age as CWD.)

Site	Unfiltered Data	Coefficient	Std. Error
Southern Tasmania (wet eucalypt forest)	n = 111		
	TSD ($p < 0.0001$)	-0.0055	0.0008
	Diameter ($p < 0.0001$)	0.0031	0.0007
	Temperature ($p = 0.0499$)	0.0288	0.0145
NSW South Coast (wet eucalypt forest)	n = 48		
	TSD ($p = 0.0189$)	-0.0051	0.0021
	Altitude ($p < 0.0001$)	0.0051	0.0011
	Slope ($p = 0.0015$)	0.0373	0.0111
Wet Eucalypt Forests (Southern Tasmania + NSW South Coast)	n = 159		
	TSD ($p < 0.0001$)	-0.0059	0.0007
	Diameter ($p < 0.0001$)	0.0033	0.0006
	Rainfall ($p = 0.0258$)	-0.0002	0.0001
Central Queensland (dry eucalypt woodland)	n = 88		
	TSD ($p < 0.0001$)	0.0070	0.0015
	Species ($p = 0.0026$)	-0.1017	0.0327
Far North Queensland (tropical rainforest)	n = 41		
	TSD ($p = 0.0151$)	-0.0335	0.0132

4.5 ORIENTATION BIAS OF CWD STUDIED

Orientation bias was checked by calculating the difference in direction of the CWD piece and the aspect direction (directly downhill), known as Δ-angle, and comparing this against the slope (see section 3.4.1.2 *Correction for Bias in Orientation* for a discussion of the theory behind this method).

As can be seen by the even scattering in Figure 4-20, there is no visual evidence of orientation bias at any of the forest and woodland areas surveyed. There was no Δ-angle vs slope analysis for the NSW sampling, as the decision to test for orientation bias was made after the sampling in NSW had been completed. It is assumed that there is no CWD orientation bias at the NSW sampling area, as there was no bias found in the sampling area of southern Tasmania, which has a similar forest type (wet eucalypt forest) and similar slope values.

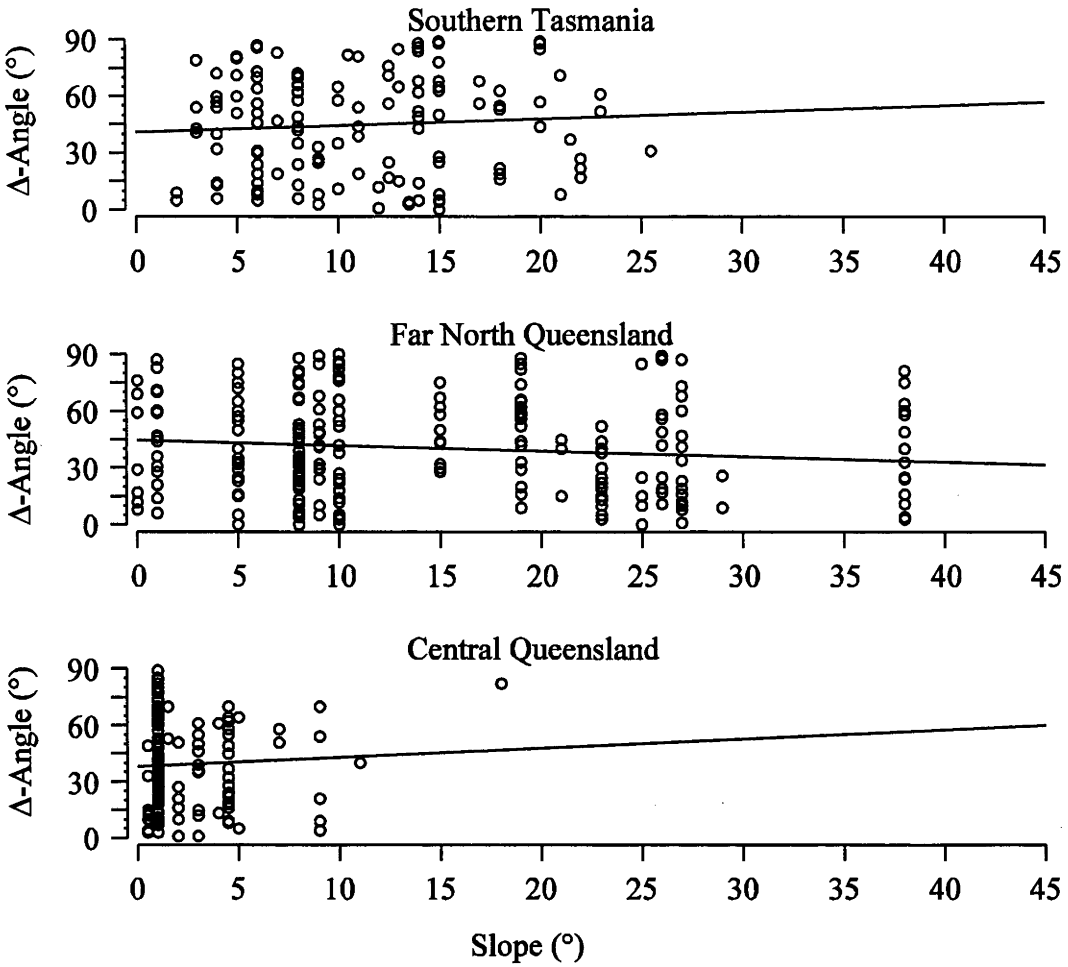


Figure 4-20. Graph of Δ-angle vs. Slope. There is no evidence of significant orientation bias in the CWD direction, as the values are evenly spread throughout the range of slopes encountered in each region.

Table 4-8. Values from straight-line regression check for orientation bias of CWD samples. All fitted lines are not significantly different from a horizontal line, indicating that there is no orientation bias in the CWD study areas.

State Region	*n*	Intercept	Slope	*p*-value
Southern Tasmania	129	40.743	0.360	0.399
Far North Queensland	257	44.667	-0.293	0.063
Central Queensland	142	37.894	0.490	0.531

A straight-line model was fitted to the Δ-angle and slope data, to check for significance in orientation bias. All fitted slopes were not significantly different from a horizontal-line (see Table 4-8), indicating that there was no orientation bias evident in the CWD for the areas studied. A re-analysis of the central Queensland data, with the

sample at Slope = 18° removed due to the potential for disproportionately high influence, resulted in a less-significant departure from a horizontal-line ($p = 0.707$).

If trees were to roll downhill after falling, then they may not be oriented in the direction of the slope. This would not lead to any orientation bias by itself, as it would reduce the likelihood of CWD being oriented directly downhill. Therefore, movement of wood after falling is not considered to increase bias in any manner.

CHAPTER 5

DISCUSSION

5.1 DISCUSSION OF PROJECT RESULTS

This chapter discusses the results found from analyses of sample-data collected from both fieldwork and laboratory work. The results are discussed separately, and in comparison with the findings of other investigators as discussed in the Literature Review chapter. The contribution of the results of this project and the literature review are thoroughly discussed in the context of the application toward the management of CWD in natural and managed forested environments.

The discussion of CWD management involves justification and strategies for preserving amounts of CWD as close to natural levels as possible, as well as the potential for eucalypt CWD in respect to carbon sequestration and trading. The discussion on CWD management also encapsulates strategies for maintaining CWD-reserves in production-forest estates, as well as strategies for CWD recovery in areas that have been converted to ecosystem parks and reserves.

Implications of excessively-low amounts of CWD in the environment are discussed with respect to impacts on nutrient cycling, habitat availability, and potential for localised extinctions of organisms requiring naturally-high amounts of CWD.

5.1.1 DECAY CLASSES OF CWD

Decay classification systems were developed for the wet eucalypt forest CWD of southern Tasmania, the dry eucalypt woodland of central Queensland, and the wet tropical rainforest of far north Queensland, using cluster analyses (see section 4.1 *Decay Classes of CWD*).

For each of the three sampling-regions, each with its own ecosystem type (wet eucalypt forest, dry eucalypt woodland, wet tropical rainforest), the most appropriate decay-class system was a five-class system.

The benefit gained from using cluster analysis to produce a decay-classification system is shown in Figure 4-4. The statistically-derived (*pam* cluster analysis) system, based on the external attributes of *E. obliqua* samples collected, provided a more-symmetrical frequency distribution of samples than did the subjective human-derived system currently in use by Forestry Tasmania (see Figure 4-4).

However, the cluster analysis was dominated by logs less than 45 cm in diameter (99 logs < 45 cm compared to 12 logs > 45 cm) and this may result in the classification system being biased towards smaller-diameter logs. Sollins (1982) found that decay-stage classification systems were affected by log diameter; where a system that worked well with smaller-diameter logs did not perform well with larger-diameter logs, and *vice versa*. Consequently, usage of the derived decay-classification system must be used with caution, as it may prove problematic/ineffectual for large-diameter eucalypt logs.

The decay-stage classification system developed in this project should prove to be more efficient in classification of eucalypt CWD than the currently-used subjective systems. This system removes some of the possible confusion that may occur with logs being classified with a subjective system, as there is less onus placed on the surveyor to pass judgement into which decay-class a log belongs (as there are clearly-defined classification criteria), increasing both speed and accuracy of assessment. The decay-classification method (see section 4.1.1 *Determination of Decay Classes*) created in this project is also very flexible, in that it can be used to classify the eucalypt CWD into a predetermined number of decay classes. (Note the method used to derive the decay-classification system has not been shown as it contains several steps and employs multiple software-packages.) An example of the flexibility of this method has already been shown in the original determination of a 5-class system for the southern Tasmanian sampling, where it was found that the most-decayed stage was not encountered, so the fifth-stage (most decayed) was derived subjectively, and the first four stages were derived using the samples collected.

5.1.2 DECAY RATES

Proportional decay-rates were calculated for the wet eucalypt forest regions of south-coastal NSW and southern Tasmania, and for the tropical rainforest of far north Queensland. Unfortunately, as the densities of the central Queensland dry eucalypt-woodland CWD did not exhibit a density-decrease with time (see Figure 4-10), a decay-rate could not be established for the central Queensland CWD.

5.1.2.1 Wet Eucalypt Forest CWD Decay Rates

The similarity of the decay rates of the wet eucalypt forests, of southern Tasmania and south coastal New South Wales (see section 4.2 *Decay Rates* and Figure 4-12) was

somewhat surprising considering the southern Tasmanian CWD was a single species (*E. obliqua*), and the NSW CWD was mixed-species eucalypt forest. Of course, this does not mean that the combined-data decay rate for the two regions is representative of all wet eucalypt forest species, as each major type of wet eucalypt forest (either mixed species or single-species dominated) will need to be assessed to determine whether a representative rate-of-decay can be used 'across the board'. It is very unlikely there will be a single representative rate-of-decay that can be prescribed to the wet eucalypt forest ecosystems, as there is likely to be a large difference in decay rates among all wet eucalypt forest types.

5.1.2.2 Wet Tropical Rainforest CWD Decay Rates

The calculated SEM *k*-value ($k = 0.1121$ yr^{-1}) for the tropical rainforest CWD of far north Queensland may include several sources of error. Firstly, there were only 40 samples used in the determination of the decay-model constant; this unfortunate low *n*-value was due to few trees in the inventory-plots having calculable ages. Secondly, ages were determined by medians between presence-and-absence from records of succeeding inventory-sampling, which are exposed to potential errors of age-overestimation; for a thorough discussion of the pitfalls of using median-dates between presence-and-absence records see section 2.2.4 *Chronosequence and Repeated Measures Studies*. Thirdly, as the tropical rainforest samples decay faster (much faster than the wet eucalypt-forest samples collected) it is likely that the analyses were dominated by relatively longer-lasting (slower-decaying) samples. (Longer-lasting CWD is more likely to be encountered than faster-decaying CWD, which may bias the sample-collection toward slower-decaying samples.) Whilst the first point above may have an unbiased affect on whether it shows a higher or lower error in determining the rate-of-decay for these rainforest CWD, the second and third points will bias the calculated decay rate to a slower rate-of-decay than actually exists in these wet tropical rainforests.

However, the calculated *k*-value ($k = 0.1121$ yr^{-1}) does fall between the $k = 0.19$ yr^{-1} of Chambers *et al.* (2000), for standing dead trees (SDTs), and $k = 0.106$ yr^{-1} of Clark *et al.* (2002), for CWD and stumps, for their tropical rainforest studies.

5.1.3 AMOUNT OF CWD IN THE ENVIRONMENT

5.1.3.1 CWD Environmental Volumes

Mean-volumes of CWD were 7.7 m^3 ha^{-1} for the dry eucalypt woodland of subtropical central Queensland, 46.2 m^3 ha^{-1} for the wet rainforest of tropical far north Queensland, 51.5 m^3 ha^{-1} for the wet eucalypt forest of warm-temperate south coastal NSW, and 731.6 m^3 ha^{-1} for the wet eucalypt forest of temperate southern Tasmania.

The mean CWD volume-loading for central Queensland (7.7 m^3 ha^{-1}) was less than half the mean-loading (18.53 m^3 ha^{-1}) found by Woldendorp *et al.* (2002b, 2004); whose eucalypt-woodland sites were all located at Injune (Queensland). The discrepancy may be the result of this survey being conducted on sites located on cattle-stations, which covered a large geographic-area. Due to the requirement for sites with CWD of known-age, which were gleaned from fence-construction and land-clearing records from lease-holders and owners of pastoral land, the CWD surveys were also conducted on cattle-station land, and the history of clearing and disturbance by cattle may have created a lowered volume-loading for these sites. The dry eucalypt woodlands of central Queensland are very disturbed environments, and this makes generalisations regarding natural conditions, and CWD loading, very difficult. Areas of relatively undisturbed woodland exist in the western Top End of the Northern Territory, where European colonisation was minimal before the land (Arnhem Land) was returned to Aboriginal-ownership, and it is recommended that sampling from these areas (if permission could be obtained) should be done before any generalisation be made as to CWD-dynamics of natural eucalypt woodland.

The mean CWD volume-loading for the tropical rainforest sites of far north Queensland (46.2 m^3 ha^{-1}) was about twice that of the mean-loading (28.22 m^3 ha^{-1}) found by Grove (2001); despite the minimum-diameter threshold of Grove (2001) being smaller at 7.5 cm (compared to the 10 cm minimum threshold of this study). The sites studied here included coastal, montane (up to 1200 m; Mt. Fisher), and inland sites, whereas Grove's (2001) sites, whilst in the same general area, were all coastal sites (maximum altitude was 140m); of the 13 sites surveyed in the tropical rainforest, 11 were at altitudes higher than the maximum altitude of Grove (2001). The discrepancy may be due to the inclusion of inland and montane rainforest sites in this survey, and possibly past logging-activity in the area.

The mean CWD volume-loading for the mixed-eucalypt forest of south-coastal NSW was calculated to be 51.5 m^3 ha^{-1}; measured in Benandarah State Forest and southern

Murramarang National Park (which was formerly the eastern-portion of Benandarah State Forest). This mean-value is much lower than the mean-value of 100.29 m^3 ha^{-1} measured by Woldendorp *et al.* (2002b, 2004) at Kiola (mixed-eucalypt forest), and the mean-value of 196.58 m^3 ha^{-1} measured by Chee (1999) for *E. delegatensis* R.T. Baker forest at Bargo State Forest. One reason for the almost-fourfold difference between this study and that of Chee (1999) is that this study employed a minimum-diameter threshold of 10 cm, and Chee (1999) used a minimum-threshold of 2.5 cm. However, the almost doubled volume-loading of Woldendorp *et al.* (2002b, 2004) was attained using a larger minimum-diameter threshold of 15 cm, which would have been expected to show a lower volume-loading. Woldendorp *et al.* (2002b, 2004) did use direct measurement, but this is very unlikely to have resulted in the different volume-loading measurements. The discrepancies may be based on geographic differences, species differences, as well as possible logging-histories (these areas have been logged in the past, and there may have been differences in thinning-methods employed in the regenerating forests, and some collection-removal of CWD has taken place).

There were 11 categories (Forestry Tasmania forest-classification system) of eucalypt forest sampled in southern Tasmania. Of 53 transects run, 11 had calculated CWD volume-loadings exceeding 1000 m^3 ha^{-1}; nine out of 45 for mature eucalypt forest, and two out of eight for regrowth eucalypt forest with some mature trees. The highest loading calculated for any transect was 2199.4 m^3 ha^{-1}, for a mature eucalypt forest stand, and the lowest loading was 86.8 m^3 ha^{-1} also for a mature eucalypt forest stand. Mean volumes for different-class forests ranged from 1161.6 m^3 ha^{-1} down to 163.1 m^3 ha^{-1}, both for mature eucalypt forest classes. The mean volume-loading of 731.6 m^3 ha^{-1} is considerably less than the mean value of 1198.2 m^3 ha^{-1} found by Woldendorp *et al.* (2002b, 2004). The discrepancy may be due to the different sampling methods employed, as this study used 53 line-intersect transects (covering 11 different classes of wet eucalypt forest), and the study of Woldendorp *et al.* (2002b, 2004) extensively sampled three large (each 1 ha in size) plots using direct-measurement of CWD pieces. This project covered a greater range of forest-class-types, and, consequently, had a greater range of mean-volumes for forest types (163.15 m^3 ha^{-1} to 1161.62 m^3 ha^{-1}) compared to the range (744.1 m^3 ha^{-1} to 1614.7 m^3 ha^{-1}) found by Woldendorp *et al.* (2002b, 2004). What must be noted, however, is that the different forest-classes surveyed by the line-intersect method was not deemed to be representative of all possible wet eucalypt forest types in southern Tasmania, nor are the proportions of the different forest-classes surveyed representative

of the proportions of the different eucalypt forest types of southern Tasmania. Therefore, neither this project nor the work of Woldendorp *et al.* (2002b, 2004) can be interpreted as indicative of the wet eucalypt forests of southern Tasmania. This project, and the work of Woldendorp *et al.* (2002b, 2004) are the only studies that highlight some of the many different types of wet eucalypt forest in southern Tasmania, and in doing so highlight the extremely-high CWD loadings of the wet eucalypt forests in natural (minimal anthropogenic disturbance) settings. Much more research is needed before effective generalisations can be accepted for the wet eucalypt forests of both Tasmania and mainland Australia.

Eucalypt forests dominate the highest angiosperm CWD volumes in the literature, with the highest non-eucalypt CWD volume-loading reported for angiosperm forests being 135.9 m^3 ha^{-1} for a tropical rainforest in Ecuador (Gale 2000). Whilst these wet eucalypt forest CWD volume-loadings are considerably higher than the highest non-eucalypt forest loading of Gale (2000), they are comparable to the higher loadings of conifer forest ecosystems. Harmon *et al.* (1987) reported a CWD volume of 1104.5 m^3 ha^{-1} for riparian conifer forest, and Means *et al.* (1992) reported a loading of 756 m^3 ha^{-1} for a *P. menziesii* dominated forest; both studies from western USA.

5.1.3.2 CWD Environmental Mass

The mean CWD-mass calculated for the different environmental-regions were 13.2 Mg ha^{-1} for the tropical rainforest of far north Queensland, 5.8 Mg ha^{-1} for the eucalypt woodland of central Queensland, 26.7 Mg ha^{-1} for the wet eucalypt forest of south-coastal NSW, and 342.8 Mg ha^{-1} for the wet eucalypt forest of southern Tasmania. (See section 4.3.5 *CWD Environmental Amounts by Decay Class* for a breakdown of CWD environmental mass by decay classes.)

The mean CWD mass-loading for the tropical rainforest of far north Queensland (13.2 Mg ha^{-1}) is almost double the 7.23 Mg ha^{-1} calculated by Grove (2001). This corresponds to this project's calculated volume-loading being about twice that of Grove (2001); reasons for the difference are given in the previous section.

The mean mass-loading for central Queensland (5.8 Mg ha^{-1}) was only slightly less than the 7.83 Mg ha^{-1} found by Woldendorp *et al.* (2002b, 2004). This is somewhat surprising, since the volume measured in this project was less than half that measured by Woldendorp *et al.* (2002b, 2004). Reasons for the difference, obviously a result of a

higher mean wood-density found in this project, are most likely species-related; with some difference in the mean wood-density possibly also from slower growth-rates.

The mean CWD mass-loading for the eucalypt forest of south-coastal NSW (26.7 Mg ha^{-1}) was about half of that (43.64 Mg ha^{-1} and 54.74 Mg ha^{-1}) found by Woldendorp *et al.* (2002b, 2004) in mixed-eucalypt forest, and Chee (1999) in *E. delegatensis* forest, respectively.

The mean mass-loading of CWD for the wet eucalypt forest of southern Tasmania, 342.8 Mg ha^{-1}, was less than the mass-loading of 446.85 Mg ha^{-1} calculated by Woldendorp *et al.* (2002b, 2004). The discrepancy between the mean mass-loading values is similar in proportion to the discrepancy between the mean volume-loadings, and the reasons for the discrepancy would be the same as given in the previous section for the wet eucalypt forests of southern Tasmania.

The three highest non-eucalypt mass-loadings reported (in the literature read) for angiosperm CWD is 138 Mg ha^{-1}, 85 Mg ha^{-1}, 59 Mg ha^{-1} reported by Idol *et al.* (2001) for mixed oak (*Quercus*) and hickory (*Carya*) forests in the eastern USA (Indiana). The next highest non-eucalypt angiosperm CWD mass-loading reported is 58.1 Mg ha^{-1} for *Nothofagus pumilio* (Poepp. *et* Endl.) Krasser (Frangi *et al.* 1997) from old-growth forest in the far south of South America. The highest reported conifer forest CWD mass-loadings are 383 Mg ha^{-1} (Harmon *et al.* 1987), 185 Mg ha^{-1} (Means *et al.* 1992), and 179 Mg ha^{-1} (Harmon and Hua 1991); Means *et al.* (1992) also reported a CWD mass-loading of 222 Mg ha^{-1} for a conifer-dominated mixed angiosperm-conifer forest (all of these conifer-studies are from the western United States).

5.1.3.3 CWD Environmental Carbon Dynamics

The amount of carbon sequestered in CWD was calculated as 50% of the wood mass, and, as such, the values are half that of the calculated CWD mass-loadings. Consequently, the mean CWD C-loadings are 6.6, 2.9, 13.3, and 171.4 Mg C ha^{-1} for the tropical rainforest (far north Queensland), dry eucalypt woodland (central Queensland), and wet eucalypt forest of south-coastal NSW and southern Tasmania respectively.

Due to the inability to calculate a rate-of-decay for the central Queensland woodland eucalypts, C release-and-retention could not be calculated. However, using the decay-model constants and the C-mass in the CWD, calculated C-release to the surrounding environment was calculated as 738.4 kg C ha^{-1} yr^{-1} (0.738 4 Mg C ha^{-1}

yr^{-1}), 73.80 kg C ha^{-1} yr^{-1} (0.073 80 Mg C ha^{-1} yr^{-1}), and 1.239 Mg C ha^{-1} yr^{-1} respectively for the CWD of far north Queensland (tropical rainforest), south-coastal NSW (wet warm-temperate eucalypt forest), and southern Tasmania (wet temperate eucalypt forest) respectively.

Looking at the C-dynamics from a C-sequestration viewpoint, the amount of C retained in the CWD can be calculated as the original-mass less the C released to the surrounding environment. Consequently, assuming steady-state inputs and decay, the annual C-mass retained by the CWD in the different regions is 5.849, 13.25, and 170.2 Mg ha^{-1} for the CWD of far north Queensland (tropical rainforest), and the wet eucalypt forests of south-coastal NSW and southern Tasmania respectively. What is evident, in this respect, is that whilst the C-release by the CWD of southern Tasmania is high (1.239 Mg ha^{-1} yr^{-1}), it is a very small proportion of the amount of C being retained by the CWD of these wet eucalypt forests. This shows the enormous potential for C to be sequestered in the CWD of these wet eucalypt forests if they are allowed to retain 'natural' loadings of CWD.

5.1.3.4 CWD Environmental Amounts by Decay Class

Due to problems encountered using a decay-class system from the literature, which was based on northern-hemisphere studies, the CWD of south-coastal NSW was not graded into decay-classes. After this problem was encountered, it was decided to incorporate recordings of log-attributes during sampling, and to use these to derive a *post hoc* decay-classification scheme for each forest type, and to code each sample before analyses. (See section 4.1 *Decay Classes of CWD* for a description of the derivation of the decay-classification system used for each forest type.)

The frequency-distributions for the intersected-CWD in the transect surveys (see Figure 4-8) were markedly different. The southern Tasmanian CWD showed a unimodal-distribution with the central-classes having the greatest number of intersected-logs. The CWD of the central Queensland dry eucalypt woodland exhibited a bimodal-distribution, with the central-class having the lowest number of logs intersected. However, the only nine transects (each a 300 m equilateral-triangle) were run in the central Queensland sampling, and these sites were very disturbed. The tropical rainforest CWD showed a distribution with a trend of increasing numbers of intersected logs toward the latter decay classes (class-V logs accounted for more than 40% of the intersected logs). This older-has-more pattern may be due to the faster decay rates of the tropical rainforest CWD coupled with the even-aged nature of

undisturbed tropical rainforests. This means that there are always logs on the ground, and the residence-time of the logs is longer in the latter-decay-stages; in the fast-decaying-environment, the logs spend relatively little time in the earlier-decay-stages where the labile-material is quickly degraded.

5.1.4 EUCALYPT CWD NUTRIENT CONTRIBUTION

Assaying chemical concentrations in CWD collected was planned as part of this project, but, due to unforeseen circumstances, these analyses could not be done within this project. Consequently, to provide some measure of potential contribution of eucalypt CWD to native forest ecosystems, it was decided to extract maximum values of N, P, K, Ca, and Mg concentrations, for angiosperm CWD from the literature, and convert it to mass-per-area. This has been done using the southern Tasmanian CWD data, as this is where the most undisturbed sites existed (mean CWD volume-loading = 731.6 m^3 ha^{-1}; see sections 4.3.1 *CWD Environmental Volumes* and 5.1.3.1 *CWD Environmental Volumes*).

Nutrient concentrations used are the maximum concentrations for N, P, K, Ca, and Mg, and are those from sections 2.1.4.1 to 2.1.4.5. However, the maximum Mg concentration given in section 2.1.4.5 is for a conifer, therefore extraction of the maximum angiosperm Mg concentration from the literature-metadata was used; this is 32.52 µg Mg cm^{-3} (for *Populus tremuloides*; from Alban and Pastor 1993).

Nutrient concentrations calculated were (i) N = 2.351 Mg N ha^{-1}, (ii) P = 5.398 Mg P ha^{-1}, (iii) K = 553.1 kg K ha^{-1} (0.553 1 Mg K ha^{-1}), (iv) Ca = 2.334 Mg Ca ha^{-1}, and (v) Mg = 23.70 kg Mg ha^{-1} (0.023 70 Mg Mg ha^{-1}). It is very unlikely that the values from the literature are directly transferable to eucalypt CWD, however, in the present situation where data for eucalypt CWD chemical concentrations are unavailable, the maximum-values reported in the literature are used as an example of 'maximum' potential nutrient contribution to the wet eucalypt forest ecosystem.

5.1.4.1 Nutrient Dynamics in CWD Decomposition Modelling

Despite the values here being subjective, they do emphasise the potential CWD can contribute to nutrient cycling within native eucalypt forest ecosystems, especially where nutrients increase over time (see section 2.1.4 *Nutrient Cycling* for details of this point). Of major significance is the increase in nitrogen as N is sequestered from the atmosphere by N_2-fixing bacteria resident within the CWD. If CWD are removed from the ecosystem, it not only removes the N within the log, but also deprives the ecosystem

of any N that would be fixed during the time the logs would have existed after their removal.

The lack of existing information for eucalypt CWD nutrient concentrations is another example of the many knowledge gaps concerning Australian CWD. Although eucalypt decomposition can be adequately described with the empirical single-exponential model, the contribution of CWD to ecosystem functioning as it proceeds through the decomposition process can only be adequately done with the use of a mechanistic model. However, such a mechanistic model that adequately describes eucalypt CWD decomposition and interactions with the forest environment will take many years and much research to construct. Given the current knowledge that proves CWD is an important component of eucalypt forest ecosystems, it is imperative that further research on CWD decomposition dynamics be done as a matter of urgency. The mechanistic model should also include stochastic events that occur irregularly and with varying intensity (such as fire), and are not immediately apparent upon the formation of the CWD (do not occur until some time after the tree falls to the ground), making the mechanistic model somewhat of a process model. It is reasonable to expect that a comprehensive and working mechanistic model of Australian CWD decomposition dynamics would further highlight the importance of CWD to natural forest ecosystems.

5.1.5 MULTIPLE REGRESSION ANALYSES

All multiple regression analyses (MRA) showed that time-since-death (TSD) was significantly correlated with sample wood-density (see section 4.4 *Multiple Regression Analyses*). (This section is referring to Table 4-7 of section 4.4.7 *Summary of Multiple Regression Analyses*) This is a case in point of 'stating-the-obvious'; as this result should be expected, as the density will change with decay, and the samples will take-time-to-decay.

5.1.5.1 Wet Eucalypt Forests

The results of the MRA showed that time-since-death (TSD), diameter, and rainfall were significant (all $p<0.026$) with respect to sample wood-density, for the wet eucalypt forests; southern Tasmanian (South Tasmania) and south-coastal New South Wales (NSW South Coast) sampling areas. However, this is an inter-regional analysis, which covers two areas that are separated by both latitude and climate (southern Tasmania is cool-temperate, whilst south-coastal NSW is warm-temperate).

SOUTHERN TASMANIA

The MRA for southern Tasmania shows TSD ($p<0.0001$), diameter ($p<0.0001$) and temperature ($p=0.0449$) significantly correlated with change in sample wood-density with decay. The significant affects of TSD are discussed above.

Due to the prevailing wet-climate, it is not expected that moisture-availability (*viz.* rainfall) would play a significant role in CWD decay, as it is unlikely that moisture-availability would have a long-term affect on decay. However, in the cool-temperate climate of the region, the cold winter winds blowing from the Southern Ocean would undoubtedly affect the heat-availability for the decomposer organisms, and it is expected that temperature would play a significant part in determining decomposition rates in this region.

Diameter also had a significant affect on wood density with respect to sample wood-density, but this affect is complex, and hard to interpret, as diameter may be acting as a covariate for several driving-factors affecting CWD decay. Firstly, it may simply be a factor of larger-diameter CWD taking longer to be fully-colonise by decomposer organisms, and therefore affecting the density-decrease. (It is unlikely that it is insulating against severe moisture-deficiency, as rainfall was not a significant factor in the MRA.) Secondly, the significantly diameter-effect may be expressing differences in wood-density between initial sapwood and heartwood proportions. Thirdly, larger-diameter CWD has a lower surface-area:volume ratio, and it may take longer for the toxins to be leached. Fourthly, it may be showing that larger-diameter CWD is insulating the inner-environment against temperature extremes, especially in summer; in which case it is acting as a covariate with the temperature-effect (which was also found to be significant), and therefore causing a confounding-of-factors in the analysis. Without specific/targeted further research into the driving-variables of *E. obliqua* CWD-decay dynamics, it is impossible to determine which factors are responsible for the significant diameter-effect on *E. obliqua* decay.

SOUTH-COASTAL NEW SOUTH WALES

The MRA for New South Wales shows TSD ($p=0.0189$), altitude ($p<0.0001$) and slope ($p=0.0015$) significantly correlated with change in sample wood-density with decay. The significant affects of TSD are discussed above.

The significant affect of altitude is surprising, as the hills are not very high. However, the ridge-tops have vegetation that is more dry-tolerant than the gullies

between the hills; with the ridge-tops typically having vegetation such as stringy-barks and small-leaved shrubs, the mid-ridges having spotted-gum (*Corymbia maculata* (Hook.) K.D. Hill & L.A. Johnson) among other eucalypts, and cycads (*Macrozamia communis* L.A.S. Johnson), and the gullies having blue-gums, tree ferns, and larger-leaved shrubs. This shows a moisture gradient from the dryer ridge-tops to the wetter gullies. Consequently, in this case, the significant altitude-effect is acting as a covariate for slope position, as affecting soil-moisture availability, which in turn is expressing the hydrological-dynamics of the terrain.

The significant-effect of slope is also expressing the hydrological-dynamics of the terrain, as the greater the slope, the greater the drainage of soil-moisture. The south-coastal NSW region had the steepest slopes encountered during the eucalypt-sampling phase of this project, with slopes up to 22.5°; only the tropical rainforest of far north Queensland had terrain with higher slopes.

Unlike southern Tasmania, with its colder-climate, that shows diameter and heat-availability to be significant factors in CWD decay, the warmer and drier environment of the south-coastal NSW CWD shows that moisture-availability (not in rainfall, but in high soil-moisture drainage) is the major limiting-resource for CWD decay.

DISCUSSION OF WET EUCALYPT FORESTS

Combining the two wet eucalypt forest regions together (southern Tasmania and south-coastal NSW), provides insight into the latitudinal and climatic affects on these ecosystems that are not evident by studying the regions in isolation. The colder and wetter environment of Tasmania shows heat-availability to be significantly limiting to CWD decay, and the warmer and drier environment of south-coastal NSW shows moisture-availability to be significantly limiting to CWD decay.

The southern Tasmanian CWD also showed a significant affect of diameter with respect to decay, but the reason for this is inconclusive, due to the possibility of diameter being a covariate for several other factors.

5.1.5.2 Central Queensland

Despite the lack of evidence for decay in the central Queensland eucalypt CWD, the MRA did show that TSD ($p<0.0001$) and species ($p=0.0026$) was significantly correlated with density change. Unfortunately, as there was a lack of evidence for

CWD decomposition, it is difficult to interpret these results, other than to say that the species difference may be an artefact of studying two species; the species-significance may not be evident if there were more species studied. (Unfortunately, this sampling-region could provide only two species with adequate samples of known ages.)

5.1.5.3 Far North Queensland

The MRA for far north Queensland showed that only TSD was significantly correlated (p=0.0151) with change in density, and therefore, significantly correlated with CWD decay. This shows that in the wet tropics, the more-moderate rainforest environment makes determination of significant factors affecting CWD decomposition more difficult, and that other factors not studied may be contributing to a greater extent than in the eucalypt forest environments studied at higher latitudes.

5.1.6 ORIENTATION BIAS OF CWD STUDIED

As the graphs of Figure 4-20 show there was not a detectible orientation-bias in the CWD surveyed; therefore, it was deemed redundant to pursue further analyses using directional-distribution statistics. (The orientation-bias was checked to see if there was a significant decrease in the difference between orientation of CWD pieces and aspect, which is the direction of greatest slope, as slope increased. In all cases, p>0.05, signifying that there was not a significant decrease in the difference between the CWD orientation and down-slope aspect with increasing slope.) Orientation bias was checked for the wet eucalypt forest of southern Tasmania, dry eucalypt woodland of central Queensland, and the tropical rainforest of far north Queensland; data for directional-bias analyses was not included in the sampling scheme until after the south-coastal NSW sampling had been completed. Woldedorp *et al.* (2002b, 2004) also found a general lack of orientation bias in the CWD of eucalypt forests.

5.2 COMPARISON OF CWD STUDIED AND LITERATURE

5.2.1 COMPARISON OF DECAY RATES

Of interest is that decay of eucalypts in the forests studied was shown to be slower than any non-eucalypt angiosperm species listed in the literature. Indeed, the decay rates of the eucalypts studied are more akin to the slow-decaying conifers.

Mackensen and Bauhus (1999, 2003) calculated the fastest decomposition rate for *Eucalyptus* (SEM decay-model constant of k = 0.0407; $t_{0.95}$ = 74 yr). Mackensen *et al.* (2003) claim that *E. regnans* CWD can lose 95% of original-mass in 7 yr, but this value

was taken from Da Costa (1979), which was a laboratory study using wood-blocks in glass-jars, with samples lying on and in the soil, which was saturated to 60% of soil-mass. Consequently, the $t_{0.95}$ of 7 yr by Mackensen *et al.* (2003) is not directly applicable to whole-logs lying on the forest floor. The $t_{0.95}$ = 74 yr of Mackensen and Bauhus (1999, 2003) for *E. regnans* is in contrast with the evidence of Gilbert (1958) whom shows a photograph of an *E. regnans* log that is at least 150-years-old, and still maintaining its shape (see Figure 1.17 of Gilbert 1958). The *E. regnans* studied by Mackensen and Bauhus (1999, 2003) used *E. regnans* wood up to a maximum age of 12 yr, and it is likely that very little degradation of recalcitrant-material (e.g. lignin) occurred during this time, and they were measuring the decay rate of the labile-material (e.g. cellulose). It must be noted, however, that the study of Mackensen and Bauhus (1999, 2003) was for samples with a diameter in the range of 10 cm to 30 cm, whereas the picture of Gilbert (1958) is of a log of considerably-larger diameter. However, this discrepancy shows the danger of only using relatively-young samples for decay-rate determination, especially if there is a likelihood of being a considerable difference in rate-of-decay between the labile and recalcitrant components; Mackensen and Bauhus (1999) stated that sapwood usually decays faster than heartwood, so their analysis may have been strongly biased toward the decay-rate of the sapwood. It would be advantageous for *E. regnans* CWD to be investigated further, with much older samples included in the sampling strategy.

The main reason for differing decay rates as determined from different studies is due to the differences between the species studied (Abbott and Crossley 1982). However, amount of decay prior to the tree becoming CWD and microclimate differences, even within the same piece of wood, along with different diameters used, all contribute to the determination of different decomposition rates (Lambert *et al.* 1980).

5.2.1.1 Discussion of Decay Rate Comparisons

This thesis only reports results (see section 4.2 *Decay Rates*) using the single-exponential model of decay (SEM), as the double-exponential model (DEM) was rejected on philosophical grounds (for a discussion of problems with the DEM see section 2.2.5.8 *Discussion — Comparison of Models*). However, due to the recent popularity of the DEM, comparisons of the SEM and DEM are provided in Appendix D. (This study of the slow-decaying eucalypts showed the DEM is not useful for describing decay dynamics of CWD with a slow rate-of-decay; see section 2.2.5.8.)

While Næsset (1999b) noted that the natural situation for *P. abies* (a conifer) trees to fall with their branches attached, which causes a slower decay rate due to the elevation of the log, this is not applicable to most eucalypts, as the forest eucalypts do not have side branches; they only possess branches in the crown. Therefore, the greater majority of a forest eucalypt will be in contact with the soil upon falling. Indeed, lower limb retention is rare for forest angiosperm-trees, and a slow decomposition rate due to elevation would be relatively rare in the angiosperms compared to the conifers.

The lack of any trend in decay (using wood-density) over time for the central Queensland CWD (see Figure 4-10), is viewed a result of the harsh environment of the dry eucalypt woodlands of central Queensland. The wood was more affected by weathering (fragmentation) and subsequent incorporation into the soil than due to decomposition above the soil surface. Termite-mounds were seen growing around SDTs in the central Queensland woodland sites (*pers obs.*). In a study of litter decomposition, in the northern Chihuahuan Desert region of New Mexico (USA), Moorhead and Reynolds (1991) found that the decomposition of woody material on the surface was primarily driven by abiotic weathering and termite activity, whereas subsurface decomposition was driven by micro-organisms. The study of Moorhead and Reynolds (1991) is very similar to the findings of the central Queensland CWD decomposition-dynamics, and may be indicative of the decomposition/weathering of CWD in open-environments that are predominantly hot and dry.

5.2.2 COMPARISON OF CWD VOLUMES

The sample collection and measurement of environmental-loadings of CWD, of this study were done in areas with very different past disturbance régimes. The central Queensland eucalypt woodland is a very disturbed environment, with a history of land clearing for pastoralism, as well as the effects of cattle browsing within the remaining woodland environments. The south-coastal NSW eucalypt forest sites were located within areas that are currently within (Benandarah State Forest) or were previously within (southern Murramarang National Park; which was formerly a part of Benandarah State Forest), which are production forests. The sample collection for the southern Tasmanian CWD was conducted in areas that had been logged in the past. These sites were necessary for the eucalypt sampling, as they provided samples with known-age; which is necessary for the determination of the decay rates. However, the line-intersect-transects for southern Tasmania were conducted in many eucalypt-forest types, including mature eucalypt forest. The far north Queensland tropical rainforest

samples and line-intersect-transects were conducted in research plots that do not have a history of anthropogenic disturbance. The above must be acknowledged in respect to the values reported in this work, as site history (past disturbance-type and ecosystem-management) can influence the relative pool-sizes of the CWD (Currie and Nadelhoffer 2002).

5.2.3 LITERATURE METADATA ISSUES AND RECOMMENDATIONS

An attempt was made to perform analyses upon metadata extracted from the literature. However, due to differences in metadata presented, there were not enough metadata to obtain meaningful results from multiple-regression analyses (MRA). Only obvious correlations could be analysed, as incomplete records for lesser-studied parameters could not be analysed due to null-values in some fields excluding records from the MRA. (Due to the requirement of S-PLUS to have values in all 'cells' of each parameter for all replicates, the desired analyses often resulted in too few replicates for analyses.) However, there was enough data to perform a *t*-test on the single-exponential model constants (*k*-values) for angiosperms and conifers, as presented in section 2.1.1.6.

A major problem in performing the literature-metadata analyses was the inconsistency in the definition of coarse woody debris. It would be beneficial to use only fallen timber in the definition-class of CWD; as standing timber is not debris. The separation of fallen-wood and standing dead trees (SDTs) also allows the two groups to be analysed separately. Although some studies are only concerned with the amount of dead-wood, such as in inventory surveys, other studies are concerned with habitat availability, and there is a need to know stocks of prostrate-debris and standing dead-trees. It would only require one extra tick-box on a survey form to designate whether the wood-piece is elevated or prostrate during inventory surveys, and very little extra work to separate these different components when reporting values in the literature.

An inconsistency that was somewhat annoying in extracting the chemical literature-metadata was the different formats employed in reporting CWD chemical concentrations, these were either (i) mass per volume (e.g. g cm^{-3}), (ii) mass per area covered by CWD (e.g. g m^{-2}), (iii) percent of CWD mass (e.g. % mass/mass), or (iv) percent of original concentration remaining. The reason for differing formats in reporting chemical concentrations is due to differing objectives in analysing the CWD wood. However, in most cases, the information for mass-per-volume of chemical concentrations would be known during the analyses, and it would be beneficial if the

chemical concentration were additionally reported in mass-per-volume (g cm^{-3}) as a standard method of reporting CWD chemical concentrations.

It is unfortunate that CWD metadata is presented in differing formats, as this makes extraction of metadata slow and often incomplete. If maximum gain is to be obtained from the metadata presented in the CWD literature, then some means of standardisation is essential (this may be achieved through the 'CWD message board' medium on the internet; see **http://groups.yahoo.com/group/dead_wood/messages/1**). Metadata analyses have the potential to provide the benefit of analyses from a large number of studies, but standardisation must be achieved in order to maximise benefits from metadata analyses.

5.3 PROBLEMS WITH AVAILABLE DATA

5.3.1 HIGH VARIABILITY OF DATA COLLECTED

High data variability is a problem with density determination of decay rates, and is an inherent problem with the chronosequence method of sample collection (see section 2.2.4 *Chronosequence and Repeated-Measures Studies* for a discussion of these points). The high variability of the relative densities of the samples collected makes statistical analyses difficult, and detracts somewhat from the inferences from the data analyses. Unfortunately, high variability is an entrenched problem with studies of CWD decomposition, and is a product of the complexity of the decay process (Means *et al.* 1985, Næsset 1999b). Climate has an undoubted affect on CWD decomposition (Næsset 1999b); however, the decomposition process is also affected by non-climatic factors (Brown *et al.* 1998; Delaney *et al.* 1998). Climate can also affect the CWD density indirectly as trees that grow at different rates will tend to have different wood-densities (Næsset 1999a). Problems with high-variability with sample wood-density have been encountered by other investigators (e.g. Graham and Cromack 1982; Barber and Van Lear 1984; Næsset 1999a; Clark *et al.* 2002). CWD decomposition is heterogeneous (Mattson *et al.* 1987), and this undoubtedly causes the high-variability in wood-density.

Even a single log can exhibit marked heterogeneity of decay (Schowalter 1992; Pyle and Brown 1999). It is likely that some of the wood-density data variability, of the samples collected in this study, is due to individual logs having different rates of decay in different parts of the log; despite the log being the same age for its entire length. Consequently, the exact density of the collected sample depends on the region of the log

from where the sample was taken (Graham and Cromack 1982). This pattern of differential decay was also encountered by Lambert *et al.* (1980) studying the conifer *A. balsamea* in the north-eastern United States and by Schowalter (1992) and Pyle and Brown (1999) studying angiosperms. Swift *et al.* (1976) in a study of branch decay also encountered highly variable decomposition.

Bias in sample collection was eliminated by taking the sample disc from the midsection of the bole that was visible. This in itself contributed to variability in the density of the samples collected, as some sample-discs were taken from log-sections in contact with the ground, and others from sections that were not in direct contact with the ground at the point of sample collection.

Quite marked heterogeneity of decay can exist between two similar logs lying in close proximity (Graham 1925; Næsset 1999a), which may be due to species, microsite, or mode-of-death differences (Brown *et al.* 1998; Delaney *et al.* 1998). All collected samples were from separate logs, and all logs were independent of other logs; no logs from stacked collections (clumps/windrows) of logs were sampled, as these were all assumed to be from anthropogenic activities where the logs were pushed into windrows for post-logging burning. Collecting samples from isolated logs undoubtedly created a situation where maximum variability would be encountered between the samples from the logging coupe/compartment. (Due to contextual reasons, only one disc was collected from each log, which also allows assumption of independence between samples. Additionally, due to some logs being short (less than 2 m in length) due to the nature of logging slash, it would have been impossible to take more than one sample from all logs; and different numbers of samples from different logs may have induced bias.) However, while collecting samples from within windrows would undoubtedly reduce variability, the windrows are an artificial (anthropogenic-created) environment, and do not reflect the natural spatial arrangement of CWD. The windrow-logs could also be expected to have a higher-than-natural decay rate, due to the majority of the logs being shaded, and protected from the wind, by the logs above them; resulting in a generally more benign decay-environment (higher moisture availability and a more moderate temperature régime).

Coarse woody debris loadings can be extremely variable within a single forest (Spies and Cline 1988). Given the heterogeneity that exists between logs (and even within single logs) within a forest, it is not surprising that there can be considerable

heterogeneity in between-stand decomposition-rates due to variability in factors that control CWD decomposition (Næsset 1999a).

A major problem for this project was the lack of *a priori* eucalypt decomposition data. The lack of potential target samples which could be aged accurately was a major obstacle, especially the lack of older samples which could be accurately aged. This lack of older samples led to the problem of sample sites of close ages being sampled, and this in turn led to a great deal of overlap between sample ages. From the data collected during this project, it is recommended that eucalypt samples with age gaps of at least 10 years should be sought, although finding reliable data which can age samples beyond 50 years in extremely scarce.

Another problem leading to the high variability in the sample data is the past practice of selective logging, which meant that several decades after logging, the slash was near impossible to distinguish from CWD that had formed prior to the area being logged.

Due to the problems associated with using the median date, between last forestry inventory measurement of a particular tree and the next survey period when the tree was not recorded (assumed to have fallen during the intervening time period), to age CWD, it is recommended that fallen trees be recorded as such. (See section 2.2.4 *Chronosequence and Repeated-Measures Studies* for a discussion of the problems associated with non-recording of fallen trees.) Recording of fallen trees will allow them to be separated from trees that were missed during the survey, although they were alive and standing. This will improve the accuracy of estimating the age of the CWD, with a resulting decrease in variability.

Dendrochronology can be a useful tool for chronological studies Brown *et al.* (1998). Unfortunately, it has been generally accepted that few eucalypt species exhibit distinct annual-growth-rings, and dendrochronology has limited use for ageing eucalypt samples; although this tenet may be more to do with incorrect analytical procedures than with the ring-anatomy of the ecualypts themselves (Brookhouse 2006).

5.3.2 POOR CORRELATION OF DECAY WITH AVAILABLE CLIMATIC DATA

The climate-data used in the modelling of the far north Queensland tropical rainforest sites were obtained from historical site-data obtained from the Commonwealth Scientific and Industrial Research Organisation at their Tropical Forest Research Centre in Atherton (Queensland). The climate-data used for the central Queensland, south-coastal NSW, and southern Tasmanian modelling were obtained

using the interpolation-software ANUSPLIN, from the Centre for Resource and Environmental Studies (CRES); based at The Australian National University. For further explanation of the climate-data used, see section 3.1 *Study Sites*. Unfortunately, this method was the only method available for obtaining climatic data for all sites, as very few meteorological stations were located in the vicinity of the sampling sites; due to their remoteness.

An alternative sampling strategy would be to restrict sampling to sites where meteorological stations are within close proximity to the proposed sampling sites. However, due to the paucity of available age-data, which is required for the modelling, sampling was restricted to sites with little, or no, directly-available data. This forced the use of climate models to provide climate data, and the generalised nature of the values obtained from the model resulted in poor correlation with the decay process occurring in the CWD.

5.4 IMPLICATIONS OF CLEARFELLING ON CWD MANAGEMENT

5.4.1 STANDING DEAD TREE LIMITATION

The impact of logging creates a greater proportion of logs, compared to standing dead trees (SDTs), than is the natural occurrence of mass tree mortality. Predominantly, soil movement and wind damage create logs from living trees, whereas pathogen infection, fire, insect attack, etc. create SDTs. The impact of clearfelling causes a large proportion of the coarse woody mass to bypass the SDT stage, depriving SDT-dependent species of potential habitats, especially the larger diameter SDTs. Clearfelling, mass soil-movement, and windthrow, can be thought of as 'mechanical-disturbance', as it not only kills the trees, but also causes them to change physical position (*viz.* falling to the ground). Mechanical-disturbance creates a pulse of CWD, from living trees, that would be expected to have similar decay-dynamics, and would create a cohort of CWD that passes through the decay-stages (decay-classes) synchronously. The kill-only disturbances would kill the trees, but not cause them to fall to the ground because of the vector of tree death. This creates many SDTs, that will decay slowly compared to the prostrate CWD, and would also fall at different times (often due to very localised wind gusts), consequently this would create heterogeneity of decay-state amongst the CWD pieces within a forest ecosystem, adding to the structural complexity that would exist in a natural forest environment.

5.4.2 SHORT-ROTATION LOGGING IMPACTS

Repeated short-rotation clearcutting, as occurs in Australia, prevents growth of large trees (Applegate 1989; Lindenmayer *et al.* 1999), resulting in a cessation of inputs of large-CWD (Spies and Cline 1988; Stevenson *et al.* 2006). Consequently, production forests have less larger-diameter CWD, with a corresponding reduction in size-heterogeneity, than unmanaged forests (Lindenmayer *et al.* 1999; Debeljak 2006).

Short-rotation logging depletes CWD stocks (Spies *et al.* 1988; Jurgensen *et al.* 1997; Sturtevant *et al.* 1997), which in turn reduces the structural complexity of the forest ecosystem, as the structural-complexity contributed by CWD is reduced (Spies and Cline 1988). The smaller-diameter CWD decays faster (Spies and Cline 1988), not only reducing amount of CWD, but also reducing the time each log is available to contribute to ecosystem functioning. Eaton and Lawrence (2006), studying a dry tropical forest in southern Mexico, found that CWD mass-loading declined with forest age, as each time the forest were cleared they had lowered stocks of trees, which contributed less CWD each time the forest is cleared; reducing standing-biomass from natural amounts will reduce the amount of CWD available in the ecosystem in the future (Hodge and Peterken 1998). However, this is to be expected with anthropogenic-clearing, as the CWD from old forests is decaying, and the newer regenerating-forests are unlikely to achieve large trees due to the regularity of clearing, consequently, limiting CWD inputs (Eaton and Lawrence 2006).

Bader *et al.* (1995) found species richness of decomposer-fungi is reduced with increasing harvesting rate, as the shorter the logging rotation, the lower the species richness of the fungi present; as species richness increases with age.

The reduced average diameter of the CWD, which comes with increasing harvesting rates (shorter-rotation logging), is also detrimental to species richness; as larger-diameter logs have been found to have higher species richness (Söderström 1988; Andersson and Hytteborn 1991; Bader *et al.* 1995). This reduced species richness may be, to some extent, linked to the reduced diameter of CWD under the short-term logging rotation, as larger-diameter logs provide a reserve of longer-lasting nutrient stores than do smaller-diameter logs (Spetich *et al.* 1999). (Sections 2.1.1.3 *Controlling Factors of Decomposition* and 5.8.1.2 *Importance of CWD Age, Amount, and Diameter, in Management* provide thorough discussions on the importance of CWD diameter.)

One of the problems with short-rotation logging-régimes is that the post-logging burn removes fine-litter (organic matter), to provide nutrients for the regenerating forest.

Whilst this is a natural process in itself, the short-rotation fires are too frequent (the interval is unnaturally-short), and the result is less organic-matter being incorporated into the forest soil. This reduced organic-matter in the soil may lead to increased drainage of the soil, especially in sites with steeper slopes, and this may eventually lead to a change in the botanical community to a dryer forest-type, even if rainfall remains steady or even increases. This may cause areas with 'wet' vegetation-communities, such as eucalypt forest with tree fern and rainforest understorey, to change to one with a dry-tolerant understorey community. The south-coastal NSW area sampled showed marked heterogeneity in vegetation communities, based on the relevant vertical-position on the ridge (ridge-top *vs.* mid-ridge *vs.* gully), and this type of mosaic of small botanical-communities may become common in areas where currently there is extensive wet eucalypt forest with a rainforest and tree fern understorey. (See section 5.1.5 *Multiple Regression Analyses* for a discussion of the floristic heterogeneity of the NSW sampling area.) Of course, this change is not caused by short-rotation logging practices *per se*, but the post-logging burn; the same effect would be caused by any unnaturally-frequent fire-régime in the wet eucalypt forests, such as caused by repeated lighting of fires by arsonists. The associated change-in-environment, with resultant change in vegetation-community may reduce decay rates in resident CWD, as the microclimate would be drier, which will increase the time nutrients are immobilised in the CWD. The drier CWD would detrimentally affect the resident decomposer organisms, and this would be the main factor reducing the decay rate. The drier CWD would likely have lowered N accumulation, as the N_2-fixing bacteria within the CWD require anaerobic conditions in order to fix atmospheric nitrogen; and anaerobic conditions occur in CWD with high moisture content.

5.5 IMPLICATIONS OF WOOD REMOVAL ON CWD MANAGEMENT

5.5.1 CWD REMOVAL

Slow decay rates generally result in a higher steady-state loading of CWD (MacMillan 1981). In the past, CWD was often considered an obstructive-hindrance to regeneration of a forest after logging (Triska and Cromack 1980). However, contemporary knowledge has shown that CWD can help seedlings become established.

Management strategies that allow for the removal of CWD can lead to a decisive reduction of the CWD load in the managed area. (Although licensed removal is regulated, much wood is removed by people for personal usage, such as firewood.) This is evidenced by the NSW sites having a slightly slower decay rate than the

southern Tasmania sites (although the difference is not significant), yet having a much lower CWD loading than the Tasmanian sites. Most of the NSW sites have only recently (1st January 2001) been incorporated into Murramarang National Park, and can be expected to increase in CWD loading over the next century or so; due to reduction in CWD removal.

CWD contains many nutrients, and is often a site for nutrient-sequestration (see section 2.1.4 *Nutrient Cycling* for further discussion on nutrient-dynamics of CWD). Retention of CWD on-site will, to some extent, reduce the impacts of the nutrients removed in logging operations. The retention of nutrients on-site is important, as eucalypt forests are generally nutrient poor, as eucalypt-forest litterfall often contains lower nutrient concentrations than other forest types (Attiwill *et al.* 1978). Bader *et al.* (1995) recommend leaving some CWD on-site after logging to facilitate dispersal of wood-inhabiting organisms between remaining patches of forest. The remaining CWD must be high quality for organism dispersal, such as large diameter CWD in different stages of decay. CWD in different stages of decay is important for forest ecosystem health (Urcelay and Robledo 2004).

5.5.2 DUMPING OF CWD INTO CLUMPS AND WINDROWS

Bulldozing CWD into clumps, or windrows, should only be done when necessary, as it exposes the decomposer organisms to greater concentrations of predators and pathogens; due to the greater concentration of potential hosts and prey. Affording a greater resource (hosts or prey) to the predators can lead to the crash of the resident decomposer organism population, which in turn can lead to a reduction of the natural decomposition rate, resulting in a reduction of the nutrient-cycling rate, ultimately leading to reduced ecosystem efficiency. Therefore, it is recommended that CWD should be left in as-close-to-natural distribution as possible, to minimise the potential for an unnatural disturbance to the predation of the decomposer organism community. For a discussion of the dynamics of the effects of higher predators/pathogens upon aggregared/clumped prey populations, see Begon *et al.* (1990; pp 321-322, 351, 352, 353), and Sinclair *et al.* (2006; p169).

5.5.3 CREATION OF CWD 'RESERVES'

The retention of CWD in forest ecosystems requires careful consideration of the functional role of CWD in the ecosystem. There are many uses of CWD to forest management, both biological and physical. Examples of the biological roles are as

habitat, shelter, and food resource. Nutrient-cycling and erosion mitigation are examples of the physical role CWD plays in the forest. This multi-faceted function of CWD to ecosystem functioning requires careful consideration when management strategies are being formulated for CWD retention. As an example, Bader *et al.* (1995) found the highest species richness of the white-rot and brown-rot decomposer fungi in the intermediate stages of decay, and the lowest species richness in the early stages of CWD decay. This requires that different age CWD, encompassing all stages of decay, should be retained on-site. Bader *et al.* (1995) also found that the species richness also depended on the distance to the nearest dispersal centre of the decomposer fungi for a given decay stage. Low dispersal ability of organisms, such as exhibited by some CWD-inhabiting insect species, make anthropogenic fragmentation of CWD habitats for these species a key threatening process (Grove 2002). This requires that the distance between areas of CWD retention be no further than the dispersal distance of the least mobile decomposer organism, or the dispersal distance for the dispersal vector (e.g., spore carrying insects).

5.6 NATURAL CWD DENSITIES IN NATIVE FORESTS

5.6.1 HOW NATURAL ARE AUSTRALIA'S NATURE RESERVES

The relatively fast growth rates of the eucalypts coupled with the slow measured decomposition rates, suggest that the steady-state loading of CWD would be high in wet eucalypt forest ecosystems devoid of anthropogenic influence. However, the wet eucalypt forest sampled in southern NSW has a much lower CWD loading than that measured in southern Tasmania. One of the major differences between the two locations is that the wet eucalypt forests of mainland Australia have been subjected to much greater anthropogenic influence from land clearing (for farming) and wood collection (for fuel-wood and building materials). It is probable that the natural loading of CWD in the mainland forests is similar to that measured in the relatively untouched forest ecosystems of southern Tasmania, but greater anthropogenic influence has resulted in a greatly reduced loading throughout the mainland forests.

It must be remembered, though, that this investigation has only studied two areas of wet eucalypt forests, and that a much greater number of forested areas need to be studied to state definitively whether the CWD of southern Tasmania, which approach 1000 m^3 ha^{-1}, are representative of the natural loading of the mainland forests. Further studies incorporating species growth rates, decomposition rates, and size and density per hectare of mature trees, are needed to check comparability between wet eucalypt forest

ecosystems. Besides this study, Lindenmayer *et al.* (1999) Woldendorp *et al.* (2002b, 2004) have found some wet eucalypt forest types have natural CWD-volumes exceeding 1000 m^3 ha^{-1}.

Despite the restricted coverage of the area of Australia covered by wet eucalypt forests, these forests have experienced a reduction in ecosystem assemblage and functioning, due to unnaturally-low loading of CWD, since European colonisation of Australia.

One of the problems of gauging the change in the wet eucalypt forest ecosystems, since European colonisation, is that the vast majority of Australia's wet eucalypt forests have experienced anthropogenic change long before the current generation of managers of nature reserves and parks. Many managers may assume that the forest they observed prior to its last logging was the natural state, when in fact that forest may have been heavily modified prior to the last logging event. Even in areas that were not logged previously, there may have been a history of aborigines and settlers collecting wood from the forests for firewood and building materials, as it would be easier to collect CWD than fell large standing trees. Consequently, what many environmental managers may view as a natural state with respect to CWD-loadings, in the wet eucalypt forests, may be erroneous, as these environments have been exposed to CWD removal at a high rate for up to two hundred years; and possibly at a lower level of removal for thousands of years.

5.6.2 IMPLICATIONS OF LOW CWD LOADINGS

The most important issue facing managers of nature parks and reserves is the attempt to regenerate a naturally functioning forest ecosystem after many years of anthropogenic degradation. An ecosystem with a high CWD loading, such as found in southern Tasmania, will have many CWD-dependent species with low dispersal ability, as they have evolved in environments where CWD is abundant (Grove 2002; Grove and Meggs 2003). When the CWD density (pieces per area) is reduced to any appreciable extent, the density-dependent poor-dispersers may not be able to colonise other CWD pieces when the current piece becomes unsuitable as a habitat, and may become locally extinct.

Although the eucalypt woodlands of Australia have a much lower basal-area of trees, and therefore, a much lower CWD loading, than the eucalypt forests, especially the wet eucalypt forests, CWD still performs an important function in these ecosystems. It has

been observed that skinks (family Scincidae) in tropical Australian eucalypt woodland use CWD as shade-shelter sites for thermoregulation and as cover for ambushing prey such as spiders (*pers obs.*). Suitably-close CWD must be maintained so that skinks can hunt effectively without risking heat stress. Removal of CWD, which is naturally sparse in these woodlands, may prevent skinks from living in many areas of woodland.

It is, therefore, vitally important to not only recognise the importance that CWD plays in ecosystem functioning, but to also recognise that the amount of CWD within a particular area is also crucially important to the functioning of a natural ecosystem.

5.7 CARBON LOADING OF CWD

In a simulation of north-west United States forests, Harmon *et al.* (1990) found that conversion of old-growth forest to faster-growing plantation-forests actually resulted in a net loss of C to the environment, due to the large amount of C stored in the old-growth forest environment. Even when taking into account the C stored in wood products from repeated-harvesting of the plantation, Harmon *et al.* (1990) found it would take in excess of 200 yr before the plantation-forest would account for the same C-storage as the old-growth forest ecosystem. This shows the value of retaining old-growth forests. The high loading of CWD found in unmanaged old forests is an important component of the C budget of forest ecosystems.

5.7.1 CONTRIBUTION OF CWD TO FOREST CARBON SEQUESTRATION

Plantinga and Birdsey (1993), in developing a carbon-budget model, assumed that logging residue, including CWD, decayed immediately, and did not contribute to ecosystem C-storage. This present study, and many other studies cited in the Literature Review chapter, show decay rates so slow that some CWD persists for centuries, and that CWD should be included in C-modelling. Appropriate decay-model constants (k-values) are available for many different species, and when a specific species is not listed in the literature, there is enough information in the literature to have an 'educated-guess' as to an appropriate rate-of-decay at the landscape scale. Policymakers and ecosystem managers require means of predicting future CWD loadings under different management strategies in order to more-effectively manage C-stores in forest ecosystems (Næsset 1999b).

The present situation of C trading in Australia excludes CWD from forest C budgets. As seen from the Results Chapter, CWD can contribute large amounts of C to the forest budget, and in disturbed areas, there is a potential for a great increase in the forest C

sequestration if CWD volumes are allowed to accumulate to natural (pre-European colonisation) levels.

5.7.2 CWD CARBON SEQUESTRATION IN WET EUCALYPT FORESTS

To test the potential for C sequestration with CWD included in the C accounting process, after clearfelling and CWD removal, it was decided that a mathematical model could be used to show the potential increase in C sequestration budgets if CWD were to be included. The modelling of CWD contribution to forest carbon accounting was done with Mathcad 2001 (MathSoft Engineering & Education, Inc 2001). *Eucalyptus obliqua* data was used for the modelling, with the growth data (supplied by Forestry Tasmania) fitted with the logistic-model of Renshaw (1995) using the *genfit* function of Mathcad, and the SEM of CWD decay from the decay-modelling using S-PLUS (see section 4.2 *Decay Rates*). *Eucalyptus obliqua* live for about 400 years (Grove *et al.* 2002).

Fire-effects on CWD were not included in the model, due to grossly-inadequate knowledge of CWD fire-dynamics. Charred logs have a reduced decay rate (USDA Forest Service 2001), however, the initial fire causes a pulse of mass-loss, albeit the extent will depend on the intensity of the fire, the moisture-content of the log, and the diameter of the log (larger-diameter logs will lose proportionally less mass than smaller-diameter logs). The greater the intensity of the fire, the greater the proportion of the log that will be lost in the fire, but the greater the moisture-loss and sterilisation of the log, resulting in a greater reduction in decay, at least in the short-term; which may, or may not, result in a long-term overall increase or decrease of decay rate. This perturbation of the decomposition-process by fire will prevent the attainment of steady-state decomposition dynamics in the long-term (Woods and Raison 1982), especially in the fire-prone eucalypt forests. Fire also kills some living trees, increasing CWD recruitment over subsequent years. The effect of fire on CWD-decomposition is extremely complex, and one that presently cannot be adequately described for meaningful inclusion in models of the decay dynamics of eucalypt-CWD due to inadequate knowledge. The model presented here only includes C stored in growing trees and CWD, and is presented purely as an exercise to highlight the amount of CWD-carbon in comparison to that of living trees.

The effect of including CWD in the carbon contribution of tree material to the carbon budget is an increase of 42%, based on the data for *E. obliqua* from southern Tasmania (see Figure 5-1). This modelling exercise, whilst an idealised-example, shows that

CWD is a major contributor to forest C budgets, and should be included in ecosystem carbon accounting.

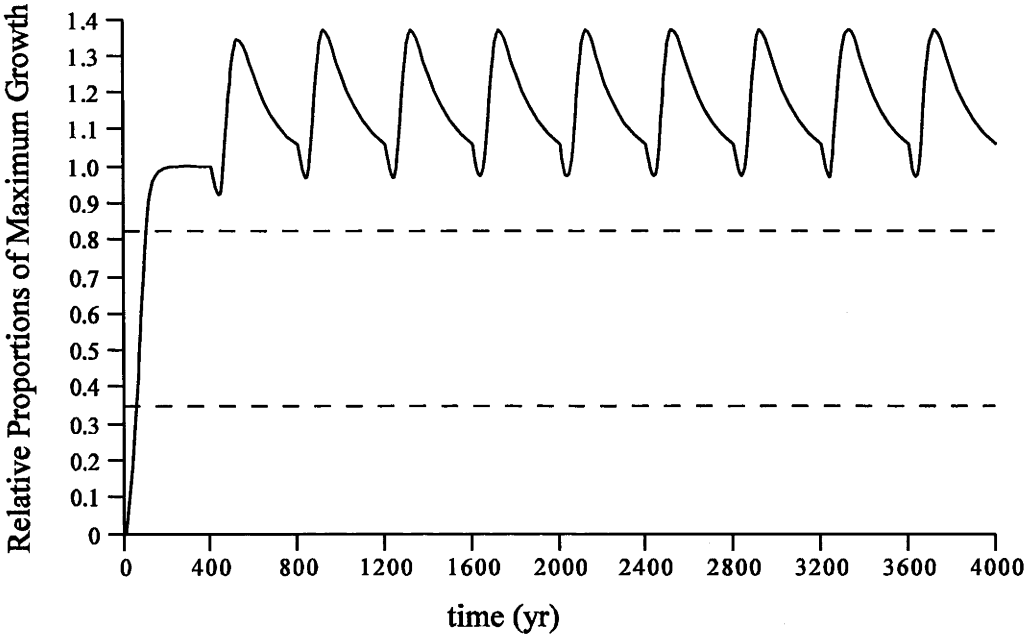


Figure 5-1. Contribution of living-trees and CWD to carbon budget of regenerated mature-forest after clearfelling and total CWD removal. Values are as a proportion of the maximum growth attained by the living-trees. Solid-line is the amount of C in living-trees and CWD as a proportion of the maximum C-mass attained by the living-trees. Upper dashed-line is the mean-value for the living-trees, and lower dashed-line is the mean-value for the CWD. The mean-value for the CWD is 42% of the mean-value for the living-trees.

Currie and Nadelhoffer (2002) suggest that the steady-state assumption should be used with extreme caution; Frissel (1981) states that the steady-state condition requirements of models are almost never met. However, if the assumption of 'steady-state' can include a representative mean-value for a consistent cyclic-pattern of variation about the mean-value, then the term 'steady-state' not only becomes applicable, it also has greater meaning. Consequently, the mean-values given in Figure 5-1 are applicable for long-term C-sequestration values, as the cycle is constant after 900 yr. However, it must be noted that the mean-values calculated from the model are arithmetic-means, and not RMS-values (quadratic-means). In this demonstrative-model, the arithmetic-mean was chosen as (i) forestry-stocking levels are usually calculated as arithmetic-means, (ii) all values are positive (the cycle does not produce negative-values), and (iii) the amplitude of the cycle is small relative to the reference-value (1.0) that represents the maximum living-tree biomass value.

In areas that have been subjected to pre-1990 logging and other forms of wood removal (such as wood collection by private individuals for fuel wood), there is great potential for C sequestration by allowing CWD to accumulate to natural levels. Whilst the proportional-increase of CWD is small per year, over an area of many hectares this may sum to a considerable amount of CWD, and will generally be an increase in C-stores that requires minimal effort on the part of land management. Indeed, the potential contribution of CWD means that it is imperative that CWD be included in C accounting and modelling (Eaton and Lawrence 2006). Unfortunately, research into the potential for CWD as a C-store is generally lacking (Chambers *et al.* 2000; Eaton and Lawrence 2006; Bütler *et al.* 2007), and this area of research has been particularly neglected in Australia (Woldendorp *et al.* 2002a).

If CWD can be included in C-trading, the additional C-sequestration provided by CWD may serve to provide additional income for bureaux and agencies involved in the management of nature parks and reserves where CWD and wood collection activities have ceased. The Kyoto Protocol to the United Nations Framework Convention on Climate Change (UNFCCC) provides mechanisms whereby terrestrial post-1990 C-sinks may be included in national greenhouse gas inventories (Keith *et al.* 2000). Article 3, paragraph 3 (Article 3.3), of the Kyoto Protocol stipulates the C sequestered since 1990 in reforested land may be included in carbon accounting. Coarse woody debris is valid for inclusion as sequestered C within the context of Article 3.3, and every attempt should be made to include increased CWD-biomass in carbon accounting, and therefore, in carbon-trading. The inclusion of CWD in C-trading would give the CWD an economic-value, providing impetus to CWD conservation, which in turn helps to maintain a higher quality of natural ecosystem functioning. The inclusion would also have beneficial impacts to management authorities of nature reserves and parks where commercial forestry has occurred; as the extra income could be used to enhance rehabilitation of the newly-protected area. A case in point here would be the former eastern-portion (east of the Princes Highway) of Benandarah State Forest that was excised (1st January 2001) into the southward expansion of Murramarang National Park in southern New South Wales.

The above-model is based on *E. obliqua* data for southern Tasmania, and is not directly transferable to other sites, or other scenarios; it is for demonstration purposes only. When modelling C-stocks at scales larger than specific site-types, site history

should be included into the model to distinguish the affect of different site-histories for different strata at these larger-scales (Currie and Nadelhoffer 2002).

5.8 MANAGEMENT OF CWD IN NATIVE FORESTS

Anthropogenic modification of natural forest ecosystems can have a long-lasting detrimental affect on natural forest functioning (Youngblood *et al.* 2006). Management practices can have a large and lasting impact on loadings of CWD (Harmon *et al.* 1990; Harmon and Hua 1991). Managed native forests generally have lowered-loadings of CWD compared to natural forest ecosystems (Spies *et al.* 1988; Hodge and Peterken 1998; Debeljak 2006). Management of CWD must be included in forest management (Lee *et al.* 1997; Sturtevant *et al.* 1997). Woldendorp *et al.* (2002a) estimate that there is about 1 Mha of commercial forest plantation established on ex-native forest land in Australia, which may contain a considerable amount of CWD.

Size-class distribution of CWD is just as important as amounts of CWD in forest environments. Hence, adequate amounts of large-diameter CWD, as well as volumes-per-hectare, must be included in the management strategy of CWD in native forests. Normal ecosystem functioning in native forests cannot be ensured if inadequate CWD loadings are maintained (Grove and Meggs 2003).

5.8.1 CWD CONTRIBUTING TO ECOSYSTEM STRUCTURAL COMPLEXITY

Coarse woody debris adds structural complexity to forest ecosystems (Harmon *et al.* 1986; Spies and Cline 1988), and old-growth forests usually have greater amounts of CWD than younger forests (Grier *et al.* 1981; Spies and Cline 1988; Sturtevant *et al.* 1997; Lindenmayer *et al.* 1999; Spetich *et al.* 1999; Woldendorp *et al.* 2002b). Older forests also have larger CWD, due to the larger trees found in older forests (Ashton 1976; Lindenmayer *et al.* 1999; Spetich *et al.* 1999). It is of no coincidence that some of the greater structural complexity of old-growth forests is derived from the greater amounts of CWD, and the greater size-diversity of CWD found in old-growth forests; especially the greater concentration of larger diameter CWD.

Maintenance of fertility in forest ecosystems is an important consideration of forest management (Moorhead *et al.* 1996). Since CWD has its highest nutrient concentration in the highly decomposed state (Fahey 1983; Idol *et al.* 2001), the CWD must be allowed to decompose completely *in situ* for the environment to realise the benefits of the release of sequestered nutrients from the CWD. Whilst the physical-structure of CWD are important for existing organisms (such as its role in providing habitat, water

storage, erosion mitigation, and refuge from fire), it is the nutrients stored, and accumulated, in CWD that potentially have the greatest influence on the ecosystem, as the released nutrients have a direct affect upon primary productivity in the forest ecosystem. A reduction in forest primary productivity will have detrimental flow-on affects to the whole forest ecosystem, and as CWD provides most nutrient-release at the end of its existence, it is important that CWD remain in the ecosystem.

5.8.1.1 Predisposition to Inner-Heartwood Rotting

Living eucalypts can often experience heart-rot (Yee *et al.* 2001), with infection gained via the exposed heartwood contained in broken branches (Wilkes 1982y). Heart-rot existing in the inner heartwood in living eucalypt trees becomes more prevalent as trees increase in age, and correspondingly increase in size (Yee *et al.* 2006). Recycling of the redundant inner-heartwood (the resilient outer-heartwood provides the structural stability of the growing eucalypt), by fungal and bacterial decomposer organisms, is a means of recycling the complex structural compounds of the inner-heartwood into simpler compounds. These simpler-compounds can then be extracted from the soil beneath the growing tree; with the extraction of these simpler-compounds being predominantly done by mycorrhizal-fungi in a symbiotic relationship with the tree. This predisposition to heart-rot, in the living eucalypt, possibly evolved as a means of allowing large trees to grow in nutrient-restricted environments; as the tree grows, the inner-heartwood lower down in the tree is 'allowed' to rot, releasing the compounds to the recycling process. As this 'recycled' material is directly beneath the tree, it is protected from leaching, to a large extent, by the tree above forming a dryer soil-matrix due to the rainwater being directed to the outside of the tree. Being directly beneath the tree, this 'recycled' material is also less likely to be scavenged by other trees, as the material is in the centre of the root system and mycorrhizal-fungal mass. This means of recycling would undoubtedly be very important for N-recycling, as the pith and adjacent inner-heartwood is higher in N concentration than the N-poor central and outer heartwood (Cowling and Merrill 1966; Merrill and Cowling 1966b). The higher N-concentration of the inner heartwood and pith undoubtedly leads to the higher decay rate of the inner heartwood in comparison to the outer heartwood; usually leading to the hollow 'wooden tubes' prevalent in decomposing eucalypt CWD (*pers. obs.*). Da Costa (1975) suggested the eucalypt predisposition to forming wooden tubes was due to greater detoxification of the older

inner heartwood. Scheffer (1957) found the conifer *T. plicata* also had greater decay-resistance in the outer heartwood in comparison to the inner heartwood.

Hollow logs are important for wildlife habitat, and large-diameter logs are suitable for larger animals, and therefore provide habitat for a greater number of species. Consequently, it is imperative that larger-diameter CWD is maintained within the native-forest environment; which only comes from allowing trees to grow to large sizes. Janzen (1976) suggested that this evolutionary predisposition of some tree species to form hollows might provide a site for accumulation of nutrients via the defecation by animals that forage outside the tree.

5.8.1.2 Importance of CWD Age, Amount, and Diameter, in Management

CWD AGE

Whiles and Grubaugh (1996) found that herpetofauna species-richness was linked to CWD decay-stage diversity in the environment. Torres (1994) found that species-richness of invertebrates increased with increasing decay of CWD. Consequently, it is imperative for older-CWD to be retained in ecosystems.

CWD AMOUNT

Due to heterogeneity of decay within a single log, individual logs may be more important for species richness and diversity than is suggested by the classifying a log into a single decay class (Pyle and Brown 1998, 1999). However, despite heterogeneity of decay within single logs, it is important to maintain CWD from all decay-classes, due to the different contribution of each decay-class to ecosystem functioning (Grove and Meggs 2003), as each decay-stage supports a different association of resident-species as well as providing different functions to the environment (Pyle and Brown 1998). Increased heterogeneity of CWD, due to the contribution of CWD to ecosystem functioning, leads to increased structural complexity of the ecosystem (Sturtevant *et al.* 1997). Bader *et al.* (1995) also found that species richness was positively correlated with the number of logs per hectare. Whiles and Grubaugh (1996) found that herpetofauna species-richness was linked to amount of CWD in the environment, as well as CWD decay-stage.

The less CWD there is in a forest stand, the less N_2-fixation occurs (Roskoski 1980). Coarse woody debris has been shown to be an important habitat for nitrogen-fixing organisms (see section 2.1.4 *Nutrient Cycling*), with resulting release of nitrogen as the

CWD is incorporated into the soil (Jurgensen *et al.* 1984). Consequently, unnaturally low loadings of CWD in forest ecosystems will have a somewhat reduced nitrogen-input. Despite the fact that there have not been any studies of nitrogen-fixation in Australian native eucalypt forests, it is certainly likely that there is cyanobacterial fixation of atmospheric-nitrogen on the log surface, and probably fixation provided by facultative anaerobic bacteria living within the CWD. Although regenerating eucalypt forests have nitrogen-inputs via the symbiotic association between *Acacia* Mill. and the N_2-fixing bacterium *Rhizobium* Frank, the *Acacia* are soon displaced as the eucalypts succeed the *Acacia*, and the maturing forest has to rely on other means of acquiring nitrogen, such as through N_2-fixing bacteria found in CWD. The current practice of logging 'waste-utilisation' whereby larger-diameter CWD is removed after logging operations have been completed (Jurgensen *et al.* 1984), is one that may lead to reduced productivity of a site in the next stand due to reduced nitrogen-fixation. While N_2-fixation within CWD is low compared to other inputs (Jurgensen *et al.* 1987), over the life of a forest stand the N_2 fixed within CWD may prove to be considerable and significant (Jurgensen *et al.* 1984). Roskoski (1980) found that N_2-fixation in a forest stand increased with amount of CWD, and also found that N_2-fixation rates were higher in larger-diameter CWD.

CWD DIAMETERS

Larger diameter CWD are important in ecosystem functioning (Grove and Meggs 2003), and therefore important in environmental management (Lindenmayer *et al.* 1999), as they provide refugia from the effects of log desiccation during prolonged dry weather, and protect the resident decomposer organisms from the heat of fires. Water-holding capacity increases with increasing CWD-diameter (Erickson *et al.* 1985), which in turn can lead to increased N_2-fixation within the log (Roskoski 1980). During drought, smaller diameter CWD may become completely desiccated, proving an unsuitable habitat for the decomposer organisms. The outer portions of larger CWD will also become desiccated, but the inner portions of the wood will still retain some moisture, and provide a suitable, whilst probably not ideal, environment for wood decomposer organisms to reside. The heat of fire may also sterilise smaller diameter CWD and the outer portions of larger CWD. The centre portions of the larger CWD, however, while still affected by some heat increase, may remain cool enough to allow some decomposer organisms to persist. In low-intensity fires, CWD may act as a shield for animals sheltering from the heat generated by fire, with larger-diameter CWD

providing a more-effective shield; Grove and Meggs (2003) found CWD provided a refuge site for beetles escaping the heat of fires in southern Tasmanian eucalypt forests.

Consequently, the refugia provided by the larger diameter CWD may provide sites for re-inoculation of smaller CWD after the cessation of unfavourable conditions. This in turn, reduces the longevity of decay cessation, or at least decay minimisation, by reducing the length of time the 'after effects' persist.

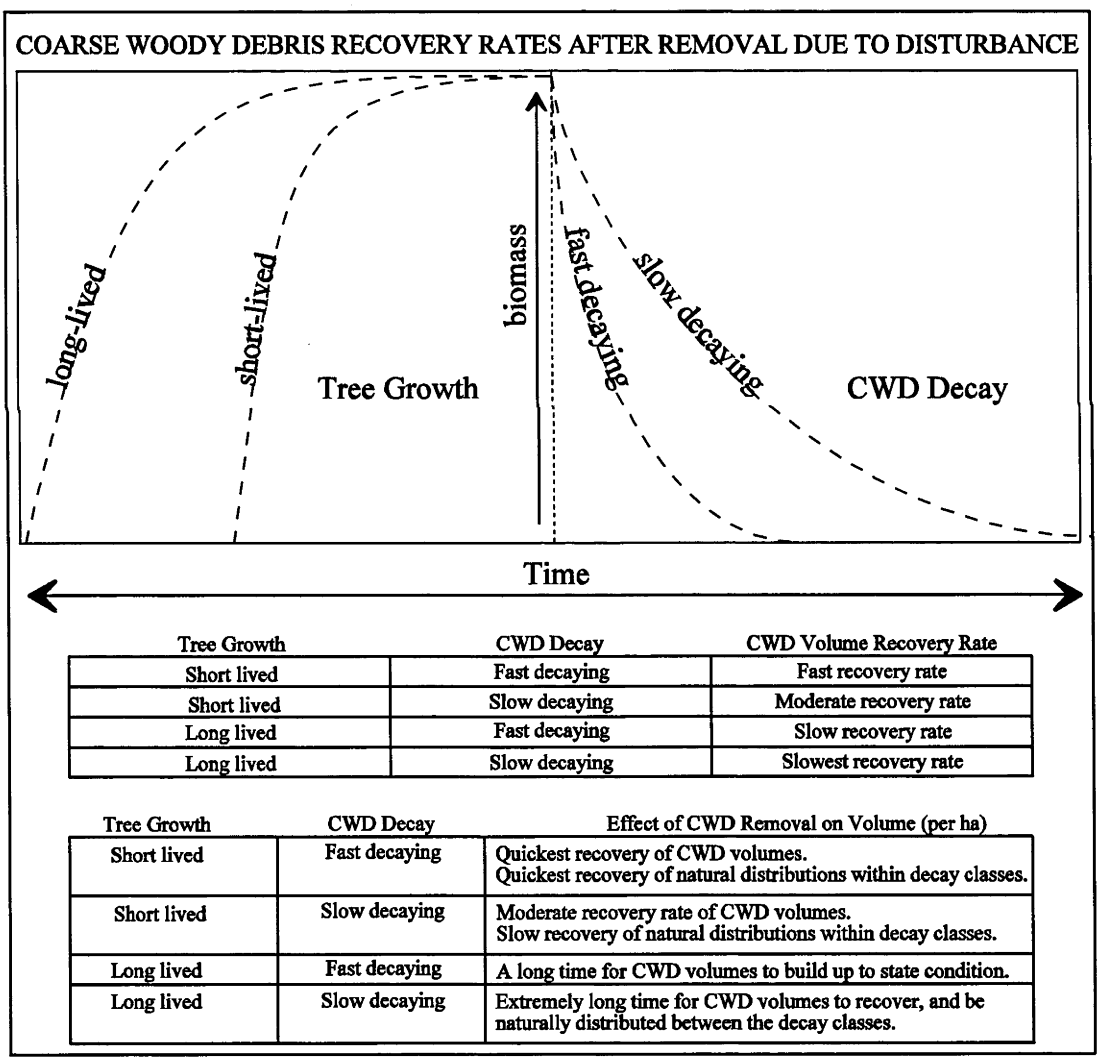
Larger-diameter logs have been found to have higher species richness of resident organisms (Söderström 1988; Andersson and Hytteborn 1991; Bader *et al.* 1995), and some organisms only occur in larger-diameter CWD (Stevenson *et al.* 2006); e.g. Yee *et al.* (2006) found that larger-diameter eucalypt logs often contain saproxylic beetles that are not found in smaller-diameter logs. Larger-diameter CWD also provides a more-stable habitat due to slower decomposition (Maser *et al.* 1988). Bader *et al.* (1995) found increasing species richness of fungi (species per log) with increasing log diameter. Urcelay and Robledo (2004), however, found that fungal species richness was higher on smaller diameter branches than on boles; although they did not distinguish between standing and fallen boles, nor did they distinguish between attached and fallen branches. Consequently, maintenance of fungal species richness in CWD will be maintained with the retention of as many large logs as possible. During drought, when smaller diameter CWD has desiccated, the moister inner wood of CWD can act as a refuge for the moisture-requiring fungi. This allows the larger diameter CWD to act as habitat for both drought-intolerant and drought-tolerant species of fungi, whereas the smaller diameter CWD can only act as habitat for the drought-tolerant fungi (Bader *et al.* 1995).

5.8.2 CWD MANAGEMENT IN NATIVE ECOSYSTEMS

The ideal management strategy for CWD is to leave it within the environment, where the tree fell. That is, leave the CWD in its natural distribution and orientation, and let it accumulate to natural volumes and decay class distributions. The organisms dependent on the CWD have evolved to suit the natural CWD distribution and volume loadings of the particular environment.

The illustration of Figure 5-2 has been constructed to show relative-times required for environmental CWD-stocks (amount in ecosystems) to recover to natural-levels after major reduction in CWD-amounts. The upper-table of Figure 5-2 lists the relative recovery-times for each of four scenarios (the longer the time arrow, the greater the

recovery time required), whilst the lower-table explicitly lists the impacts upon recovery time from a major reduction in CWD-amounts to that of natural-amounts of CWD. The upward-pointing biomass arrow of Figure 5-2 is showing the forest ecosystem recovering to maximum biomass as the forest ages — the asymptote is the maximum wood amount attained in the maturing forest, before living-trees are converted to CWD. Standing dead trees (SDTs) are to be included on the asymptote on the "Tree Growth" part (left-hand-side) of the illustration. Note, the diagram of Figure 5-2 is representing continuums, and the dashed-lines are not to be interpreted as discrete pathways, as any species or suite of species, or forest ecosystem can be represented anywhere within the trends shown by the dashed-lines.



Tree Growth	CWD Decay	CWD Volume Recovery Rate
Short lived	Fast decaying	Fast recovery rate
Short lived	Slow decaying	Moderate recovery rate
Long lived	Fast decaying	Slow recovery rate
Long lived	Slow decaying	Slowest recovery rate

Tree Growth	CWD Decay	Effect of CWD Removal on Volume (per ha)
Short lived	Fast decaying	Quickest recovery of CWD volumes. Quickest recovery of natural distributions within decay classes.
Short lived	Slow decaying	Moderate recovery rate of CWD volumes. Slow recovery of natural distributions within decay classes.
Long lived	Fast decaying	A long time for CWD volumes to build up to state condition.
Long lived	Slow decaying	Extremely long time for CWD volumes to recover, and be naturally distributed between the decay classes.

Figure 5-2. Coarse woody debris recovery time under different tree growth-rate and CWD decay-rate scenarios. The illustration is to be interpreted as an example of relative-measure only; the longer the horizontal time-arrow, the longer the time required for recovery to natural CWD amounts.

5.8.2.1 Low Dispersal Ability – Local Extinctions

In forest ecosystems that naturally have a large volume-loading of CWD representing all decay stages, the CWD-dependent organisms are unlikely to have evolved a low level of dispersal-ability, due to the plentiful CWD, and reduction of CWD-loadings to levels significantly below that found naturally is likely to lead to localised extinctions (Bader *et al.* 1995; Jonsson 2000). Even in areas where protected-reserves are a feature of forest management, if the distance between the reserves is not considered carefully, the animals dependent on CWD may not be able to move between the reserves, preventing genetic-mixing between the isolated-populations (Andrén 1997). The affects of habitat fragmentation upon the low-dispersing organisms is not only a spatial issue, temporal availability is also an important consideration (Jonsson 2000). Maintaining adequate amounts of CWD of all sizes is also important for CWD-dependent organisms that have low dispersal-ability (Grove and Meggs 2003).

In mainland Australian eucalypt forest ecosystems, any species that are dependent on high natural CWD loadings may have become locally extinct before they were identified and described, and, as such, we are unaware of the level of modification the mainland eucalypt ecosystems have experienced. Many saproxylic insect species that exist in forests with high CWD loadings are likely to have low dispersal ability (Grove 2002; Grove *et al.* 2002; Grove and Bashford 2003; Grove and Meggs 2003), and fail to persist in the ecosystem when CWD loadings are greatly diminished. Native eucalypt ecosystems may have endured much greater levels of modification than generally reported.

5.8.2.2 CWD Reserves – in Areas of Commercial Forestry

In areas of commercial forestry operations where native species are being harvested (where disturbance is a part of management practices), the creation of areas where CWD is to be retained must be thought through carefully. In forests where CWD cannot be retained in a 'natural distribution', the managers must strive to achieve the best possible management strategy available within the operational constraints. Indeed, in some instances it may be possible to change operational practices in order to achieve a better management outcome for the CWD, and create increased structural diversity within managed forests. As an example, hand planting of seedlings, which requires open land with CWD piled into windrows, may be replaced with aerial seeding, which will allow CWD to be scattered throughout the coupe.

The maintenance of random/even distribution of CWD, and random orientation of CWD, is a goal all ecosystem managers should strive to achieve, as this not only enhances the structural diversity of the resident biota, but also aids in the mitigation of soil erosion to the adjacent aquatic environments. Managers of terrestrial environments must be respectful of the surrounding environments that may be adversely affected by their management decisions (Allan 1997).

5.8.3 KNOWLEDGE REQUIRED FOR EFFECTIVE CWD MANAGEMENT

As already discussed earlier in this thesis (see sections 1.1.5 *Paucity of CWD Studies* and 1.1.6 *Need for More Research/Studies*), there is a great need for more research into CWD-dynamics, as there is a lack of knowledge generally, and dearth of knowledge for Australian CWD specifically. Besides general scientific interest, knowledge of CWD-dynamics, and the functions performed by CWD within ecosystems, is imperative for effective management of the CWD pool (Graham and Cromack 1982; Spies *et al.* 1988; Feller 1997; Sturtevant *et al.* 1997; Spetich *et al.* 1999; Keith *et al.* 2000; Tietje *et al.* 2002; Debeljak 2006; Bütler *et al.* 2007). More research is required into the impacts of management upon ecosystems, so that effective remedial action can be implemented (Lindenmayer *et al.* 1999; Debeljak 2006). It is imperative that CWD-functioning within natural ecosystems is studied, so that targets can be set when planning management-strategies to improve ecosystem functioning of CWD in disturbed ecosystems (Triska and Cromack 1980).

A major shortcoming in Australian CWD knowledge is the decomposition dynamics of CWD, as management strategies often have to use information from studies performed overseas, usually from the Northern Hemisphere. Analyses of literature-metadata found that angiosperms decay faster than conifers ($p < 0.0001$; *t*-test); see section 2.1.1 *Decomposition of CWD* and Figure 2-1). However, it was suspected that eucalypts decay slower than other angiosperms reported in the literature, due to the large natural accumulation of CWD in wet eucalypt forest ecosystems. Results of this study strongly support the assumption that eucalypts do decay slower than the angiosperms reported in the literature. It is imperative that further studies of CWD decay dynamics be conducted to fill what is currently a vast knowledge gap in eucalypt decay dynamics. This project has only provided a 'snapshot' of eucalypt decomposition dynamics along a latitudinal-gradient in eastern Australia, and much more work needs to be done on eucalypt decay dynamics (especially for ecosystems not covered in this project) before adequate knowledge is available to ecosystem managers.

Knowledge required for effective management of the CWD pool include the total amount of CWD in the ecosystem, as well as the distribution of amounts of CWD in different decay-stages, so that felling of living trees to create CWD can be planned effectively (Pyle and Brown 1998). It is important to maintain CWD loadings (amounts) in Australian native forests to near-natural levels (Grove and Meggs 2003).

In areas of production-forestry, it would be advantageous to employ a suite of harvesting-methods to ensure heterogeneity of disturbance impacts, which more-closely mimics the heterogeneity created by diverse natural disturbance events (Lindenmayer *et al.* 2000).

5.8.4 CWD MANAGEMENT STRATEGIES IN NATIVE ECOSYSTEMS

Coarse woody debris management should be incorporated into conservation plans in the management of production forests. As regenerating native forests will be used by native organisms (plants, fungi, bacteria, animals), it is imperative that some areas of post-harvest forest are left with large amounts of CWD on-site. Besides the environmental benefits of retaining CWD, it also provides physical benefits, such as retaining some nutrients on-site, and, to some extent, mitigates erosion in the early stages of forest regeneration.

Additional to providing some CWD-reserves on harvested-sites, it would also be beneficial to exempt some areas of forest from logging altogether. This then affords some CWD in a natural-setting, whereby the decay dynamics would follow natural-paths; the CWD left on-site after clearfell-harvesting, whilst extremely beneficial, may have slightly altered decay-dynamics, and this may somewhat limit its usage by native organisms. The CWD left on-site after clearfelling will receive full-insolation, due to complete canopy removal, which may increase the temperature within the log beyond the tolerance of the decay-organisms (Loman 1965; Seastedt and Crossley 1981; Whitford *et al.* 1981).

In areas of native forest parks and reserves, where logging or CWD-removal has occurred in the past, it may be necessary to fell living trees in order to increase the amount of CWD. However, the felling of living trees must be managed carefully, as it will need to be done systematically, as regenerating forests will take some time for trees to grow to large sizes, affording the opportunity to recruit larger-diameter CWD. Consequently, a comprehensively-structured management plan will need to be constructed, with a long-term strategy for periodic felling of trees. This means that

natural CWD-amounts, in relevant size-distributions and decay-states, may not be realised for many decades, or even centuries into the future. In parks and reserves, the felling of trees for CWD-enhancement must include some means of education for the public so they are aware that some trees need to be periodically felled in order to enhance ecosystem functioning; a case of the lesser of two evils.

Environmental management must continue to embrace methods that incorporate updated knowledge of CWD requirements by natural ecosystems, which will limit degradation of natural ecosystem-functioning (Whiles and Grubaugh 1996).

CHAPTER 6

CONCLUSIONS

There were several key findings in the project, and this section will start by addressing the hypotheses posed for this project (see section 1.5 *Aims and Objectives of Project*) in turn. (i) There is a difference in CWD amounts between the areas surveyed along a latitudinal gradient. (ii) There is a difference in rate-of-decay between the different forest types, with the two wet eucalypt forest regions having similar decay rates, whilst the tropical rainforest having a much faster decay rate. (iii) The different forest types release different amounts of carbon to the environment, which is a function of the different amount of CWD and the different decay rates. (iv) There is a latitudinal-effect upon decay rate, with higher latitudes having slower rates-of-decay.

It was found that the eucalypts are the slowest decaying angiosperms, and their decay dynamics appears more comparable to that of the conifer forests of north-western North America. It was found in this study that the wet eucalypt forests of SE Australia have extremely high loadings of CWD, and the only comparable high-loadings are found in the conifer forests of NW North America; this high loading of CWD in the wet eucalypt forests has also been found in other studies.

One of the major aims of this project was to develop a decay-classification system specific for the eucalypts of Australia; as eucalypt-dominated ecosystems are assumed to be distinct from ecosystems dominated by other floristic groups. With the use of a non-hierarchical cluster-analyses method, a system of decay-classification specific for use in eucalypt ecosystems was developed, and this method has proven successful in fieldwork and in stratification of data during analyses. The method used to developed the eucalypt-specific system, has also been successfully applied to the tropical rainforest CWD, and the CWD of the dry eucalypt woodland of central Queensland. The method is not only robust in being able to produce different decay-classification systems for different ecosystem types, but it can be tailored to produce decay-classifications requiring different numbers of decay-classes.

Due to the much slower decay rate of the eucalypts, compared to northern hemisphere angiosperms, the adoption of northern hemisphere standards for Australian CWD management is inappropriate. Management based on the higher decay rates of non-eucalypt angiosperms, will undoubtedly lead to severely nutrient-poor ecosystems

in managed parks and reserves. Any management decisions to reduce CWD loading in the field for the purpose of fire-fuel reduction must be based on the natural functional and structural requirements of the native eucalypt forests. It must also be recognised that CWD lying on the ground does not burn as completely as standing dead trees of similar size, and, as such, does not pose the same potential fire hazard as standing trees.

Plants gather nutrients that are being washed through the soil before they are lost from the system; however, these nutrients, as well as energy-rich compounds manufactured through photosynthesis, are locked up in the biomass of the living tree. The nutrients and energy are only made available to the general forest environment after tree death, through the process of decomposition. Removal of CWD from the forest ecosystem will result in the removal of nutrients and energy from the forest ecosystem. Unless there is a significant input of P, Mg, and Fe, and energy, then continued removal of energy and essential nutrients is unsustainable, and will inevitably result in the degradation of the forest ecosystem. CWD left in the ecosystem will somewhat dampen the loss of nutrients and energy through harvesting actions in production forests. Coarse woody debris has been shown to be a site for N_2-fixation in foreign studies, and it is highly probable that N_2-fixation occurs in eucalypt CWD.

Eucalypt forest litterfall often contains lower nutrient concentrations than other forest-types, consequently it is vital that some CWD be retained in the eucalypt forests to ensure adequate nutrients are retained on-site for effective nutrient cycling. It is also imperative that adequate amounts of CWD remain on forest floors to ensure adequate habitat and dispersion capabilities for microarthropods, as these organisms are important dispersers of decomposer micro-organisms and fungal spores. Inadequate concentrations of CWD would limit the inoculation ability of the microarthropods, causing CWD decomposition rates to decline, resulting in a decrease in the rate-of-return of CWD nutrients to the forest environment.

Coarse woody debris is also important as habitat for animals, young plants, bacteria, and fungi. Some animals use CWD as habitat for food, shelter, and ambush-sites when hunting prey. CWD has also been found to be a site for thermoregulation of exothermic animals in exposed environments. For mobile animals, it is not only important to preserve adequate amounts of CWD for their persistence, it is also important to provide adequate connectivity between clumps of CWD to afford shelter when moving between sites to minimise unnaturally high levels of predation. It is imperative for ecosystem functioning that adequate amounts of CWD, from all decay-classes and all size-classes,

be maintained in native ecosystems, especially those set aside as national parks and nature reserves.

Coarse woody debris is an important store of carbon, and should be included in C accounting of forest environments. Due to the slow decomposition of eucalypt CWD, and the large amount of CWD in wet eucalypt forests, CWD has the potential to provide some considerable increased income through carbon-trading; CWD is eligible for trading under Article 3.3 of the Kyoto Protocol. Utilising the C stored in CWD for C-trading not only gives the CWD an economic value to encourage preserving CWD in native eucalypt forests, it also has the potential to provide income to partially-offset the cost of rehabilitating areas of native forest that have experienced high levels of past anthropogenic-disturbance.

This study, and recent work by others, has shown that some of the tall wet eucalypt forests of south-eastern Australia have the highest amounts of CWD reported for any forest environments in the world. Indeed, only the wet forests of western North America have amounts of CWD comparable to the tall wet eucalypt forests of SE Australia. The implications of these naturally-occurring high CWD loadings is that the resident organisms have evolved to suit an environment with very large amounts of CWD; often exceeding 1000 m^3 ha^{-1}. Whilst some organisms in these environments will not be affected by dramatically reduced CWD loadings, it is undeniable some will be affected. Consequently, for these ecosystems to function effectively as natural environments, it is vital that managers of these environments make every effort to preserve CWD loadings to volumes as near to natural levels as possible.

Due to a lack of knowledge of the roles coarse woody debris performs in native ecosystems, it has generally been ignored in management plans of native ecosystems in Australia. However, from recent work by others, and the work contained in this project, it is evident that CWD must be included in ecosystem-management policy.

Nothing symbolises the cycling and intricacies of life better, than the usage of decaying wood by growing organisms.

> "... but those to which I allude were found, even in the drier parts of the forest, beneath logs of rotten wood, on which I believe they feed." Charles Darwin (1839), 'Voyage of the Beagle'.

REFERENCES

Abbott, D. T., and Crossley, D. A. Jr. (1982). Woody Litter Decomposition Following Clear-Cutting. *Ecology*. 63, 35-42.

Abeles, F. B., Boshart, R. P., Forrence, L. E., and Habig, W. H. (1971). Preparation and Purification of Glucanase and Chitinase from Bean Leaves. *Plant Physiology*. 47, 129-134.

Adams, D. G. (2002). The Liverwort-Cyanobacterial Symbiosis. *Biology and Environment: Proceedings of the Royal Irish Academy*. 102B, 27-29.

Adams, M. A., and Attiwill, P. M. (1984). Role of Acacia Spp. in Nutrient Balance and Cycling Regenerating *Eucalyptus regnans* F. Muell. Forests. I. Temporal Changes in Biomass and Nutrient Content. *Australian Journal of Botany*. 32, 205-215

Adams, M. A., and Attiwill, P. M. (1986). Nutrient Cycling and Nitrogen Mineralization in Eucalypt Forests of South-Eastern Australia. *Plant and Soil*. 92, 319-339.

Adl, M. S., and Gupta, V. V. S. R. (2006). Protists in Soil Ecology and Forest Nutrient Cycling. *Canadian Journal of Forest Research*. 36, 1805-1817.

Aho, P. E., Seidler, R. J., Evans, H. J., and Raju, P. N. (1974). Distribution, Enumeration, and Identification of Nitrogen-Fixing Bacteria Associated with Decay in Living White Fir Trees. *Phytopathology*. 64, 1413-1420.

Alban, D. H., and Pastor, J. (1993). Decomposition of Aspen, Spruce, and Pine Boles on Two Sites in Minnesota. *Canadian Journal of Forest Research*. 23, 1744-1749.

Albisetti, A. D. K., Brang, P., Schönenberger, W., and Bugmann, H. (2003). Decay of *Picea abies* Snag Stands on Steep Mountain Slopes. *Forestry Chronicle*. 79, 247-252.

Allan, J. D. (1997). *Stream Ecology: Structure and Function of Running Waters*. Chapman & Hall, London, UK.

Andersson, L. I., and Hytteborn, H. (1991). Bryophytes and Decaying Wood — a Comparison Between Managed and Natural Forest. *Holarctic Ecology*. 14 (2), 121-130.

Andrén, H. (1997). Habitat Fragmentation and Changes in Biodiversity. *Ecological Bulletins*. 46, 171-181.

Anon. (1983). *Rainforest Research in Queensland: A Position Paper Issued by the Queensland Department of Forestry*. Queensland Department of Forestry, 1983.

Anon. (1998). *Greenhouse Challenge Vegetation Sinks Workbook: Quantifying Carbon Sequestration in Vegetation Management Projects*. Australian Greenhouse Office, Canberra. http://www.greenhouse.gov.au/pubs/sinks.html

Applegate, G. B. (1989). Biomass of Blackbutt (*Eucalyptus pilularis* Sm.) Forests on Fraser Island. *Australian Forestry*. 52, 195-196.

Arthur, M. A., and Fahey, T. J. (1990). Mass and Nutrient Content of Decaying Boles in an Engelmann Spruce - Subalpine Fir Forest, Rocky Mountain National Park, Colorado. *Canadian Journal of Forest Research*. 20, 730-737.

Arthur, M. A., Tritton, L. M., and Fahey, T. J. (1993). Dead Bole Mass and Nutrient Remaining 23 Years After Clear-Felling of a Northern Hardwood Forest. *Canadian Journal of Forest Research*. 23, 1298-1305.

Ashton, D. H. (1975). Studies of the Litter in *Eucalyptus regnans* Forests. *Australian Journal of Botany*. 23, 413-433.

Ashton, D. H. (1976). The Development of Even-aged Stands of *Eucalyptus regnans* F. Muell. in Central Victoria. *Australian Journal of Botany*. 24, 397-414.

Ashton, D. H. (1986). Ecology of Bryophytic Communities in Mature *Eucalyptus regnans* F. Muell. Forest at Wallaby Creek, Victoria. *Australian Journal of Botany*. 34, 107-129.

Attiwill, P. M., Guthrie, H. B., and Leuning, R. (1978). Nutrient Cycling in a *Eucalyptus obliqua* (L'Hérit.) Forest. I. Litter Production and Nutrient Return. *Australian Journal of Botany*. 26, 79-91.

Attiwill, P. M., Polglase. P. J., Weston, C. J., and Adams, M. A. (1996). *Nutrient Cycling in Forests of South-Eastern Australia*. In: *Nutrition of Eucalypts* (Eds. P. M. Attiwill, and M. A. Adams. pp 191-227). CSIRO Publishing, Collingwood.

Ausmus, B. S. (1977). Regulation of Wood Decomposition Rates by Arthropod and Annelid Populations. *Ecological Bulletins*. 25, 180-192.

Bader, P., Jansson, S., and Jonsson, B. G. (1995). Wood-Inhabiting Fungi and Substratum Decline in Selectively Logged Boreal Spruce Forests. *Biological Conservation*. 72, 355-362.

Baker, T. G., and Attiwill, P. M. (1985). Above-Ground Nutrient Distribution and Cycling in *Pinus radiata* D. Don and *Eucalyptus obliqua* L'Hérit. Forests in Southeastern Australia. *Forest Ecology and Management*. 13, 41-52.

Baker, J. H., Morita, R. Y., and Anderson, N. H. (1983). Bacterial Activity Associated with the Decomposition of Woody Substrates in a Stream Sediment. *Applied and Environmental Microbiology*. 45, 516-521.

Barber, B. L., and Van Lear, D. H. (1984). Weight Loss and Nutrient Dynamics in Decomposing Woody Loblolly Pine Logging Slash. *Soil Science Society of America Journal*. 48, 906-910.

Barron, R. J. (1988). Microcolonies of Bacteria as a Nutrient Source for Lignicolous and Other Fungi. *Canadian Journal of Botany*. 66, 2505-2510.

Bate, L. J., Torgersen, T. R., Wisdom, M. J., and Garton, E. O. (2004). Performance of Sampling Methods to Estimate Log Characteristics for Wildlife. *Forest Ecology and Management*. 199, 83-102.

BCMoELP and BCMoF (1998). *Field Manual for Describing Terrestrial Ecosystems. Land Management Handbook: Number 25.* British Columbia Ministry of Forests. Victoria, British Columbia.

Beadle, N. C. W., and Costin, A. B. (1952). Ecological Classification and Nomenclature. *Proceedings of the Linnean Society of N.S.W.* 67, 61-82.

Begon, M., Harper, J. L., and Townsend, C. R. (1990). *Ecology: Individuals, Populations and Communities*, 2nd Ed. Blackwell Science, Cambridge, Massachusetts, USA.

Bell, G., Kerr, A., McNickle, D., and Woollons, R. (1996). Accuracy of the Line Intersect Method of Post-Logging Sampling Under Orientation Bias. *Forest Ecology and Management.* 84, 23-28.

Benoit, R. E., Starkey, R. L., and Basaraba, J. (1968). Effect of Purified Plant Tannin on Decomposition of Some Organic Compounds and Plant Materials. *Soil Science.* 105, 153-158.

Berg, A., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M., and Weslien, J. (1994). Threatened Plant, Animal, and Fungus Species in Swedish Forests: Distribution and Habitat Associations. *Conservation Biology.* 8 (3), 718-731.

Bergerson, F. J. (1970). The Quantitative Relationship Between Nitrogen Fixation and the Acetylene-Reduction Assay. *Australian Journal of Biological Sciences.* 23, 1015-1025.

Bergstrom, D. M., and Tweedie, C. E. (1998). A Conceptual Model for Integrative Studies of Epiphytes: Nitrogen Utilisation, a Case Study. *Australian Journal of Botany.* 46, 273-280.

Bingham, B. B., and Sawyer, J. O. (1988). Volume and Mass of Decaying Logs in an Upland Old-growth Redwood Forest. *Canadian Journal of Forest Research.* 18, 1649-1651.

Blanchette, R. A. (1991). *Deterioration in Historic and Archaeological Woods from Terrestrial Sites.* In: *Art, Biology, and Conservation: Biodeterioration of Works of Art* (Eds. R. J. Koestler, V. H. Koestler, A. E. Charola, and F. E. Nieto-Fernandez. Pp 328-347). (1991). The Metropolitan Museum of Art, New York.

Blanchette, R. A. (1995). Degradation of the Lignocellulose Complex in Wood. *Canadian Journal of Botany.* 73, S999-S1010.

Blanchette, R. A., Held, B. J., Jurgens, J. A., McNew, D. L., Harrington, T. C., Duncan, S. M., and Farrell, R. L. (2004). Wood-Destroying Soft Rot Fungi in the Historic Expedition Huts of Antarctica. *Applied and Environmental Microbiology.* 70, 1328-1335.

Boddy, L. (1983b). Carbon Dioxide Release from Decomposing Wood: Effect of Water Content and Temperature. *Soil Biology and Biochemistry.* 15, 501-510.

Boddy, L. (1983a). Microclimate and Moisture Dynamics of Wood Decomposing in Terrestrial Ecosystems. *Soil Biology and Biochemistry.* 15, 149-157.

Boddy, L, and Swift, M. J. (1983). Wood Decomposition in an Abandoned Beech and Oak Coppiced Woodland in South-East England, I. Patterns of Wood Litter Fall. *Holarctic Ecology*. 6, 320-332.

Boddy, L., and Swift, M. J. (1984). Wood Decomposition in an Abandoned Beech and Oak Coppice Woodland in SE England. III. Decomposition and Turnover of Twigs and Branches. *Holarctic Ecology*. 7, 229-238.

Boerjan, W., Ralph, J., and Baucher, M. (2003). Lignin Biosynthesis. *Annual Review of Plant Biology*. 54, 519-546.

Boller, T. (1988). Ethylene and the Regulation of Antifungal Hydrolases in Plants. *Oxford Surveys of Plant Molecular and Cell Biology*. 5, 145-174.

Bonnett, H. T., and Silvester, W. B. (1981). Specificity in the *Gunnera-Nostoc* Endosymbiosis. *New Phytologist*. 89, 121-128.

Bormann, F. H., Likens, G. E., and Melillo, J. M. (1977). Nitrogen Budget for an Aggrading Northern Hardwood Forest Ecosystem. *Science*. 196, 981-983.

Bousquet, P., Ciais, P., Miller, J. B., Dlugokenchy, E. J., Hauglustaine, D. A., Prigent, C., Van der Werf, G. R., Peylin, P., Brunke, E-G., Carouge, C., Langenfelds, R. L., Lathière, J., Papa, F., Ramonet, M., Schmidt, M., Steele, L. P., Tyler, S. C., and White, J. (2006). Contribution of Anthropogenic and Natural Sources to Atmospheric Methane Variability. *Nature*. 443, 439-443.

Brais, S., Sadi, F., Bergeron, Y., and Grenier, Y. (2005). Coarse Woody Debris Dynamics in a Post-Fire Jack Pine Chronosequence and its Relation with Site Productivity. *Forest Ecology and Management*. 220, 216-226.

Brooker, M. I. H., and Kleinig, D. A. (1999). *Field Guide to Eucalypts: Volume 1: South-eastern Australia*. Bloomings Books, Hawthorn, Victoria, Australia.

Brookhouse, M. (2006). Eucalypt Dendrochronology: Past, Present and Potential. *Australian Journal of Botany*. 54, 435-449.

Brown, J. K. (1971). A Planar Intersect Method for Sampling Fuel Volume and Surface Area. *Forest Science*. 17, 96-102.

Brown, S., Lugo, A. E., and Iverson, L. R. (1992). Processes and Lands for Sequestering Carbon in the Tropical Forest Landscape. *Water, Air, and Soil Pollution*. 64, 139-155.

Brown, S., Mo, J., McPherson, J. K., and Bell, D. T. (1996). Decomposition of Woody Debris in Western Australian Forests. *Canadian Journal of Forest Research*. 26, 954-966.

Brown, P. M., Shepperd, W. D., Mata, S. A., and McClain, D. L. (1998). Longevity of Windthrown Logs in a Subalpine Forest of Central Colorado. *Canadian Journal of Forest Research*. 28, 932-936.

Brown, J. K., Reinhardt, E. D., and Kramer, K. A. (2003). *Coarse Woody Debris: Managing Benefits and Fire Hazard in the Recovering Forest*. USDA Forestry Service, General Technical Report RMRS-GTR-105. Rocky Mountain Research

Station.

Bultman, C. R., and Southwell, C. R. (1976). Natural Resistance of Tropical American Woods to Terrestrial Wood-Destroying Organisms. *Biotropica.* 8, 71-95.

Busse, M. D. (1994). Downed Bole-Wood Decomposition in Lodgepole Pine Forests of Central Oregon. *Soil Science Society of America Journal.* 58, 221-227.

Bütler, R., Patty, L., Le Bayon, R-C., Guenat, C., and Schlaepfer, R. (2007). Log Decay of *Picea abies* in the Swiss Jura Mountains of Central Europe. *Forest Ecology and Management.* 242, 791-799.

Cain, S. A., and Sharp, A. J. (1938). Bryophytic Unions of Certain Forest Types of the Great Smoky Mountains. *American Midland Naturalist.* 20, 249-301.

Cameron, G. N., and LaPoint, T. W. (1978). Effects of Tannins on the Decomposition of Chinese Tallow Leaves by Terrestrial and Aquatic Invertebrates. *Oecologia.* 32, 349-366.

Caza, C. L. (1993). *Woody Debris in the Forests of British Columbia: A Review of the Literature and Current Research.* British Columbia Ministry of Forests. Report LMR 78.

Chambers, J. Q., Higuchi, N., Schimel, J. P., Ferreira, L. V., and Melack, J. M. (2000). Decomposition and Carbon Cycling of Dead Trees in Tropical Forests of the Central Amazon. *Oecologia.* 122, 380-388.

Chee, Y. E. (1999). *A Comparison of Carbon Budgets for a Pinus radiata Plantation and a Native Eucalyptus Forest in Bago State Forest, New South Wales.* Honours Thesis, The Australian National University.

Chojnacky, D. C., and Heath, L. S. (2002). Estimating Down Deadwood from FIA Forest Inventory Variables in Maine. *Environmental Pollution.* 116, S25-S30.

Christensen, O. (1975). Wood Litter Fall in Relation to Abscission, Environmental Factors, and the Decomposition Cycle in a Danish Oak Forest. *Oikos.* 26, 187-195.

Christensen, O. (1977). Estimation of Standing Crop and Turnover of Dead Wood in a Danish Oak Forest. *Oikos.* 28, 177-186.

Clark, D. B., Clark, D. A., Brown, S., Oberbauer, S. F., and Veldkamp, E. (2002). Stocks and Flows of Coarse Woody Debris across a Tropical Rain Forest Nutrient and Topography Gradient. *Forest Ecology and Management.* 164, 237-248.

Cooper, C. F. (1983). Carbon Storage in Managed Forests. *Canadian Journal of Forest Research.* 13, 155-166.

Coplen, T. B., Krouse, H. R., and Böhlke, J. K. (1992). Reporting of Nitrogen-Isotope Abundances. *Pure and Applied Chemistry.* 64, 907-908.

Cornaby, B. W., and Waide, J. B. (1973). Nitrogen Fixation in Decaying Chestnut Logs. *Plant and Soil.* 39, 445-448.

Cosenza, B. J., McCreary, M., Buck, J. D., and Shigo, A. L. (1970). Bacteria Associated with Discolored and Decayed Tissues in Beech, Birch, and Maple. *Phytopathology*. 60, 1547-1551.

Costermans, L. (2000). *Native Trees and Shrubs of South-Eastern Australia: Covering Areas of New South Wales, Victoria and South Australia*. New Holland Publishers (Australia) Pty Ltd, Sydney, Australia.

Cowling, E. B., and Merrill, W. (1966). Nitrogen in Wood and its Role in Wood Deterioration. *Canadian Journal of Botany*. 44, 1539-1554.

Crews, T. E. (1999). The Presence of Nitrogen Fixing Legumes in Terrestrial Communities: Evolutionary vs Ecological Considerations. *Biogeochemistry*. 46, 233-246.

Currie, W. S., and Nadelhoffer, K. J. (2002). The imprint of Land-Use History: Patterns of Carbon and Nitrogen in Downed Woody Debris at the Harvard Forest. *Ecosystems*. 5, 446-460.

Da Costa, E. W. B. (1975). *Natural Decay Resistance of Wood.* In: *Biological Transformations of Wood by Microorganisms* (Ed. W. Liese, pp 103-117). Springer-Verlag, Berlin.

Da Costa, E. W. B. (1979). Comparative Decay Resistance of Australian Timbers in Accelerated Laboratory Tests. *Australian Forestry Research*. 197, 119-135.

Daniels, L. D., Dobry, J., Klinka, K., and Feller, M. C. (1997). Determining Year of Death of Logs and Snags of *Thuja plicata* in Southwestern Coastal British Columbia. *Canadian Journal of Forest Research*. 27, 1132-1141.

Daubenmire, R., and Prusso, D. (1963). Studies of the Decomposition Rates of Tree Litter. *Ecology*. 44, 589-592.

Debeljak, M. (2006). Coarse Woody Debris in Virgin and Managed Forests. *Ecological Indicators*. 6, 733-742.

Delaney, M., Brown, S., Lugo, A. E., Torres-Lezama, A., and Quintero, N. B. (1998). The Quantity and Turnover of Dead Wood in Permanent Forest Plots in Six Life Zones of Venezuela. *Biotropica*. 30, 2-11.

Dilworth, M. J. (1966). Acetylene Reduction by Nitrogen-Fixing Preparations from *Clostridium pasteurianum*. *Biochemica et Biopysica Acta*. 127, 285-294.

Dixon, R. K., Brown, S., Houghton, R. A., Solomon, A. M., Trexler, M. C., and Wisniewski, J. (1994). Carbon Pools and Flux of Global Forest Ecosystems. *Science*. 263, 185-190.

Eamus, D., McGuinness, K, and Burrows, W. (2000). *Review of Allometric Relationships for Estimating Woody Biomass for Queensland, the Northern Territory and Western Australia*. National Carbon Accounting System, Technical Report 5a. The Australian Greenhouse Office.

Eaton, J. M., and Lawrence, D. (2006). Woody Debris Stocks and Fluxes During Succession in a Dry Tropical Forest. *Forest Ecology and Management*. 232, 46-55.

Edmonds, R. L., and Eglitis, A. (1989). The Role of Douglas-fir Beetle and Wood Borers in the Decomposition of and Nutrient Release from Douglas-fir Logs. *Canadian Journal of Forest Research.* 19, 853-859.

Edmonds, R. L., Vogt, D. J., Sandberg, D. H. and Driver, C. H. (1986). Decomposition of Douglas-fir and Red Alder Wood in Clear-Cuttings. *Canadian Journal of Forest Research.* 16, 822-831.

Edwards, P. J., and Grubb, P. J. (1977). Studies of Mineral Cycling in a Montane Rain Forest in New Guinea. I. The Distribution of Organic Matter in the Vegetation and Soil. *Journal of Ecology.* 65, 943-969.

Eggleton, P., Homathevi, R., Jeeva, D., Jones, D. T., Davies, R. G., and Maryati, M. (1997). The Species Richness and Composition of Termites (Isoptera) in Primary and Regenerating Lowland Dipterocarp Forest in Sabah, East Malaysia. *Ecotropica.* 3, 119-128.

Erickson, H. E., Edmonds, R. L., and Peterson, C. E. (1985). Decomposition of Logging Residues in Douglas-fir, Western Hemlock, Pacific Silver Fir and Ponderosa Pine Ecosystems. *Canadian Journal of Forest Research.* 15, 914-921.

Evans, C. A., Miller, E. K., and Friedland, A. J. (1998). Nitrogen Mineralization Associated with Birch and Fir Under Different Soil Moisture Regimes. *Canadian Journal of Forest Research.* 28, 1890-1898.

Fahey, T. J. (1983). Nutrient Dynamics of Above Ground Detritus in Lodgepole Pine (*Pinus contorta* ssp. *latifolia*) Ecosystems, South-Eastern Wyoming. *Ecological Monographs.* 53, 51-72.

Feller, M. C. (1997). *Coarse Woody Debris in Forests: An Overview of the Coarse Woody Debris Study and the Sicamous Creek Study Area.* In: *Sicamous Creek Silvicultural Systems Project: Workshop Proceedings* (Eds. C. Hollstedt and A. Vyse, pp 134-143.). April 24-25, 1996. Kamloops, British Columbia, Canada. British Columbia Ministry of Forests Research Program, Victoria, B.C. (Working Paper 24/1997).

Ferguson, D., K. (2005). Plant Taphonomy: Ruminations on the Past, the Present, and the Future. *Palaios.* 20, 418-428.

Findlay, W. P. K. (1934). Studies in the Physiology of Wood-Destroying Fungi: I. The Effect of Nitrogen Content upon the Rate of Decay of Timber. *Annals of Botany.* 48, 109-117.

Fogel, R., and Cromack, K. Jr. (1977). Effect of Habitat and Substrate Quality on Douglas-Fir Litter Decomposition in Western Oregon. *Canadian Journal of Botany.* 55, 1632-1640.

Foster, J. R., and Lang, G. E. (1982). Decomposition of Red Spruce and Balsam Fir Boles in the White Mountains of New Hampshire. *Canadian Journal of Forest Research.* 12, 617-626.

Frangi, J. L., Richter, L. L., Barrera, M. D., and Aloggia, M. (1997). Decomposition of *Nothofagus* Fallen Woody Debris in Forests of Tierra Del Fuego, Argentina. *Canadian Journal of Forest Research.* 27, 1095-1102.

Frankland, J. C., Ovington, J. D., and Macrae, C. (1963). Spatial and Seasonal Variations in Soil, Litter and Ground Vegetation in Some Lake District Woodlands. *Journal of Ecology*. 51, 97-112.

Franklin, J. F., Shugart, H. H., and Harmon, M. E. (1987). Tree Death as an Ecological Process: The Causes, Consequences, and Variability of Tree Mortality. *BioScience*. 37, 550-556.

Frissel, M. J. (1981). The Definition of Resistance Times in Ecological Models. *Ecological Bulletins*. 33, 117-122.

Gale, N. (2000). The Aftermath of Tree Death: Coarse Woody Debris and the Topography in Four Tropical Rainforests. *Canadian Journal of Forest Research*. 30, 1489-1493.

Ganjegunte, G. K., Condron, L. M., Clinton, P. W., Davis, M. R., and Mahieu, N. (2004). Decomposition and Nutrient Release from Radiata Pine (*Pinus radiata*) Coarse Woody Debris. *Forest Ecology and Management*. 187, 197-211.

Garden, J. G., McAlpine, C. A., Possingham, H. P., and Jones, D. N. (2007). Habitat Structure Is More Important Than Vegetation Composition for Local-Level Management of Native Terrestrial Reptile and Small Mammal Species Living In Urban Remnants: A Case Study from Brisbane, Australia. *Austral Ecology*. 32, 669-685.

Garrett, L., Davis, M., and Oliver, G. (2007). Decomposition of Coarse Woody Debris, and Methods for Determining Decay Rates. *New Zealand Journal of Forestry Science*. 37, 227-240.

Gibbons, P., Lindenmayer, D. B., Barry, S. C., and Tanton, M. T. (2000). The Effects of Slash Burning on the Mortality and Collapse of Trees Retained on Logged Sites in South-Eastern Australia. *Forest Ecology and Management*. 139, 51-61.

Gilbert, J. M. (1958). *Eucalypt – Rainforest Relationships and the Regeneration of the Eucalypts*. Ph.D. Thesis, University of Tasmania, Hobart, Tasmania.

Goldstein, J. L., and T. Swain (1965). The Inhibition of Enzymes by Tannins. *Phytochemistry*. 4, 185-192.

Gonor, J. J., Sedell, J. R., and Benner, P. A. (1988). *What We Know About Large Trees in Estuaries, in the Sea, and on Coastal Beaches*. In: *From the Forest to the Sea: A Story of Fallen Trees* (Eds. C. Maser, R. F. Tarrant, J. M. Trappe, and J. F. Franklin, pp 83-112). U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-229. Portland, Oregon.

Gosz, J. R., Likens, G. E., and Bormann, F. H. (1973). Nutrient Release from Decomposing Leaf and Branch Litter in the Hubbard Brook Forest, New Hampshire. *Ecological Monographs*. 43, 173-191.

Gove, J. H., Ringvall, A., Ståhl, G., and Ducey, M. (1999). Point Relascope Sampling of Downed Coarse Woody Debris. *Canadian Journal of Forest Research*. 29, 1718-1726.

Gove, J. H., Ducey, M. J., Ståhl, G., and Ringvall, A. (2001). Point Relascope Sampling: A New Way to Assess Downed Coarse Woody Debris. *Journal of Forestry*. 99, 4-11.

Gove, J. H., Ducey, M. J., and Valentine, H. T. (2002). Multistage Point Relascope and Randomized Branch Sampling for Downed Coarse Woody Debris Estimation. *Forest Ecology and Management*. 155, 153-162.

Graham, S. A. (1925). The Felled Tree Trunk as an Ecological Unit. *Ecology*. 6, 397-411.

Graham, R. L., and Cromack, K. C. Jr. (1982). Mass, Nutrient Content, and Decay Rate of Dead Boles in Rain Forests of Olympic National Park. *Canadian Journal of Forest Research*. 12, 511-521.

Granhall, V., and Lindberg, T. (1980). Nitrogen Input through Biological Nitrogen Fixation. *Ecological Bulletins*. 32, 333-340.

Greenberg, C. H. (2001). Response of Reptile and Amphibian Communities to Canopy Gaps Created by Wind Disturbance in the Southern Appalachians. *Forest Ecology and Management*. 148, 135-144.

Grier, C. C. (1978). A *Tsuga heterophylla* - *Picea sitchensis* Ecosystem of Coastal Oregon: Decomposition and Nutrient Balances of Fallen Logs. *Canadian Journal of Forest Research*. 8, 198-206.

Grier, C. C., and Logan, R. S. (1977). Old-Growth *Pseudotsuga menziesii* Communities of Western Oregon Watershed: Biomass Distribution and Production Budgets. *Ecological Monographs*. 47, 373-400.

Grier, C. C., Vogt, K. A., Keyes, M. R., and Edmonds, R. L. (1981). Biomass Distribution and Above- and Below-Ground Production in Young and Mature Abies amabilis Zone Ecosystems of the Washington Cascades. *Canadian Journal of Forest Research*. 11, 155-167.

Griffin, D. M. (1977). Water Potential and Wood-Decay Fungi. *Annual Revue of Phytopathology*. 15, 319-329.

Griffith, G. S., and Boddy, L. (1990). Fungal Decomposition of Attached Angiosperm Twigs: I. Decay Community Development in Ash, Beech and Oak. *New Phytologist*. 116, 407-415.

Griffith, G. S., and Boddy, L. (1991a). Fungal Decomposition of Attached Angiosperm Twigs: II. Moisture Relations of Twigs of Ash (*Fraxinus excelsior* L.). *New Phytologist*. 117, 251-258.

Griffith, G. S., and Boddy, L. (1991b). Fungal Decomposition of Attached Angiosperm Twigs: III. Effect of Water Potential and Temperature on Fungal Growth, Survival and Decay of Wood. *New Phytologist*. 117, 259-269.

Grove, S. J. (2001). Extent and Composition of Dead Wood in Australian Lowland Tropical Rainforest with Different Management Histories. *Forest Ecology and Management*. 154, 35-53.

Grove, S. J. (2002). Saproxylic Insect Ecology and the Sustainable Management of Forests. *Annual Review of Ecology and Systematics*. 33, 1-23.

Grove, S. J., and Bashford, R. (2003). Beetle Assemblages from the Warra Log-Decay Project: Insights from the First Year of Sampling. *Tasforests*. 14, 117-129.

Grove, S. J., and Meggs, J. (2003). Coarse Woody Debris Biodiversity and Management: A Review with Particular Reference to Tasmanian Wet Eucalypt Forests. *Australian Forestry*. 66, 258-272.

Grove, T. S., O'Connell, A. M., and Malajczuk, N. (1980). Effects of Fire on the Growth, Nutrient Content and Rate of Nitrogen Fixation of the Cycad *Macrozamia riedlei*. *Australian Journal of Botany*. 28, 271-281.

Grove, S., Meggs, J., and Goodwin, A. (2002). *A Review of Biodiversity Conservation Issues Relating to Coarse Woody Debris Management in the Wet Eucalypt Production Forests of Tasmania*. A Report to Forestry Tasmania, August 2002. ISBN 0 7246 4324 9

Gutiérrez, A., del Rio, J. C., Martínez-Íñigo, M. J., Martínez, M. J., and Martínez, A. T. (2002). Production of New Unsaturated Lipids during Wood Decay by Ligninolytic Basidiomycetes. *Applied and Environmental Microbiology*. 68, 1344-1350.

Hafner, S. D., and Groffman, P. M. (2005). Soil Nitrogen Cycling Under Litter and Coarse Woody Debris in a Mixed Forest in New York State. *Soil Biology and Biochemistry*. 37, 2159-2162.

Halliday, J., and Pate, J. S. (1976). Symbiotic Nitrogen Fixation by Coralloid Roots of the Cycad *Macrozamia riedlei*: Physiological Characteristics and Ecological Significance. *Australian Journal of Plant Physiology*. 3, 349-358.

Hamilton, S. D., Lawrie, A. C., Hopmans, P., and Leonard, B. V. (1991). Effects of Fuel-Reduction Burning on a *Eucalyptus obliqua* Forest Ecosystem in Victoria. *Australian Journal of Botany*. 39, 203-216.

Hansen, A. J., Spies, T. A., Swanson, F. K., and Ohmann, J. L. (1991). Conserving Biodiversity in Managed Forests: Lessons from Natural Forests. *BioScience*. 41, 382-392.

Hardy, R. W. F., Holsten, R. D., Jackson, E. K., and Burns, R. C. (1968). The Acetylene - Ethylene Assay for N_2 Fixation: Laboratory and Field Evaluation. *Plant Physiology*. 43, 1185-1207.

Hardy, R. W. F., Burns, R. C., and Holsten, R. D. (1973). Application of the Acetylene-Ethylene Assay for Measurement of Nitrogen Fixation. *Soil Biology and Biochemistry*. 5, 47-81.

Harmon, M. E. (1989). Effects of Bark Fragmentation on Plant Succession on Conifer Logs in the *Picea-Tsuga* Forests of Olympic National Park, Washington. *American Midland Naturalist*. 121, 112-124.

Harmon, M. E., and Franklin, J. F. (1989). Tree Seedlings on Logs in *Picea-Tsuga* Forests of Oregon and Washington. *Ecology*. 70, 48-59.

Harmon, M. E., and Hua, C. (1991). Coarse Woody Debris Dynamics in Two Old-Growth Ecosystems: Comparing a Deciduous Forest in China and a Conifer Forest in Oregon. *BioScience*. 41, 604-610.

Harmon, M. E., and Sexton, J. (1996). *Guidelines for Measurements of Woody Detritus in Forest Ecosystems*. Publication No. 20. US Long-term Ecological Research Network Office, University of Washington.

Harmon, M. E., Franklin, J. F., Swanson, F. G., Sollins, P., Gregory, S. V., Lattin, J. D., Anderson, N. H., Cline, S. P., Aumen, B. G., Sedell, J. R., Lienkaemper, G. W., Cromack, K. Jr., and Cummins, K. W. (1986). Ecology of Coarse Woody Debris in Temperate Ecosystems. *Advances in Ecological Research*. 15, 133-302.

Harmon, M. E., Cromack, K. Jr., and Smith, B. G. (1987). Coarse Woody Debris in Mixed-Conifer Forests, Sequoia National Park, California. *Canadian Journal of Forest Research*. 17, 1265-1272.

Harmon, M. E., Ferrell, W. K., and Franklin, J. F. (1990). Effects on Carbon Storage of Conversion of Old-Growth Forests to Young Forests. *Science*. 247, 699-702.

Harmon, M. E., Sexton, J., Caldwell, B. A., and Carpenter, S. E. (1994). Fungal Sporocarp Mediated Losses of Ca, Fe, K, Mg, N, P, and Zn from Conifer Logs in the Early Stages of Decomposition. *Canadian Journal of Forest Research*. 24, 1883-1893.

Harmon, M. E., Krankina, O. N., and Sexton, J. (2000). Decomposition Vectors: A New Approach to Estimating Woody Detritus Decomposition Dynamics. *Canadian Journal of Forest Research*. 30, 76-84.

Harper, K. T., and Pendleton, R. J. (1993). Cyanobacteria and Cyanolichens: Can They Enhance Availability of Essential Minerals for Higher Plants? *Great Basin Naturalist*. 53, 59-72.

Harvey, A. E., Larsen, M. J., and Jurgensen, M. F. (1979). Comparative Distribution of Ectomycorrhiza in Soils of Three Western Montana Forest Habitat Types. *Forest Science*. 25, 350-358.

Harvey, A. E., Larsen, M. J., Jurgensen, M. F., and Jones, E. A. (1989). Nitrogenase Activity Associated with Decayed Wood of Living Northern Idaho Conifers. *Mycologia*. 81, 765-771.

Haystead, A., Robinson, R., and Stewart, W. D. P. (1970). Nitrogenase Activity in Extracts of Heterocystous and Non-Heterocystous Blue-Green Algae. *Archives of Microbiology*. 74, 235-243.

Hély, C., Bergeron, Y., and Flannigan, M. D. (2000). Coarse Woody Debris in the Southeastern Canadian Boreal Forest: Composition and Load Variations in Relation to Stand Replacement. *Canadian Journal of Forest Research*. 30, 674-687.

Hendrickson, O. Q. (1988). Use of Acetylene Reduction for Estimating Nitrogen Fixation in Woody Debris. *Soil Science Society of America Journal*. 52, 840-844.

Hendrickson, O. Q. (1991). Abundance and Activity of N_2-Fixing Bacteria in Decaying Wood. *Canadian Journal of Forest Research*. 21, 1399-1304.

Hicks, W. T., Harmon, M. E., and Myrold, D. D. (2003). Substrate Controls on Nitrogen Fixation and Respiration in Woody Debris from the Pacific Northwest, USA. *Forest Ecology and Management*. 176, 25-35.

Hobbie, S. E., Nadelhoffer, K. J., and Högberg, P. (2002). A Synthesis: The Role of Nutrients as Constraints on Carbon Balances in Boreal and Arctic Regions. *Plant and Soil*. 242, 163-170.

Hodge, S. J., and Peterken, G. F. (1998). Deadwood in British Forests: Priorities and a Strategy. *Forestry*. 71, 99-112.

Hopkins, A. J. M., Harrison, K. S., Grove, S. J., Wardlaw, T. J., and Mohammed, C. L. (2005). Wood-Decay Fungi and Saproxylic Beetles Associated with Living *Eucalyptus obliqua* Trees: Early Results from Studies at the Warra LTER Site, Tasmania. *Tasforests*. 16, 111-125.

Houghton, R. A., Hobbie, J. E., Melillo, J. M., Moore, B., Petersen, B. J., Shaver, G. R., and Woodwell, G. M. (1983). Changes in the Carbon Content of Terrestrial Biota and Soils Between 1860 and 1980: A Net Release of CO_2 to the Atmosphere. *Ecological Monographs*. 53, 235-262.

Hulme, M. A., and Shields, J. K. (1970). Biological Control of Decay Fungi in Wood by Competition for Non-Structural Carbohydrates. *Nature*. 227, 300-301.

Hurlbert, S. H. (1984). Pseudoreplication and the Design of Ecological Field Experiments. *Ecological Monographs*. 54, 187-211.

Idol, T. W., Figler, R. A., Pope, P. E., and Ponder, F. Jr. (2001). Characterization of Coarse Woody Debris Across a 100 Year Chronosequence of Upland Oak-Hickory Forests. *Forest Ecology and Management*. 149, 153-161.

Insightful Corporation. (2001). *S-PLUS 6 for Windows*. Insightful Corporation. Seattle, WA, USA.

Intergovernmental Panel on Climate Change. (1995). *IPCC Second Assessment: Climate Change 1995*. Intergovernmental Panel on Climate Change.

Intergovernmental Panel on Climate Change. (1996). *Technologies, Policies and Measures for Mitigating Climate Change*. IPCC Technical Paper I. Intergovernmental Panel on Climate Change.

Intergovernmental Panel on Climate Change. (1997b). *An Introduction to Simple Climate Models Used in the IPCC Second Assessment Report*. IPCC Technical Paper II. Intergovernmental Panel on Climate Change.

Intergovernmental Panel on Climate Change. (1997a). *Stabilization of Atmospheric Greenhouse Gases: Physical, Biological and Socio-Economic Implications*. IPCC Technical Paper III. Intergovernmental Panel on Climate Change.

Jansen, A. Robertson, A., Thompson, L., and Wilson, A. (2003). *Development and Application of a Method for the Rapid Appraisal of Riparian Condition*. River Management Technical Guideline No. 4, Land and Water, Australia, Canberra.

Janzen, D. H. (1976). Why Tropical Trees Have Rotten Cores. *Biotropica*. 8, 110.

Jenny, H., Gessel, S. P., and Bingham, F. T. (1949). Comparative Study of Decomposition Rates of Organic Matter in Temperate and Tropical Regions. *Soil Science*. 68, 419-432.

Johnson, E. A., and Greene, D. F. (1991). A Method for Studying Dead Bole Dynamics in *Pinus contorta* var. *latifolia* - *Picea engelmannii* Forests. *Journal of Vegetation Science*. 2, 523-530.

Jonsson, B. G. (2000). Availability of Coarse Woody Debris in a Boreal Old-Growth *Picea abies* Forest. *Journal of Vegetation Science*. 11, 51-56.

Jönsson, M. T., Fraver, S., Jonsson, B. G., Dynesius, M., Rydgård, M., and Esseen, P-A. (2007). Eighteen Years of Tree Mortality and Structural Change in an Experimentally Fragmented Norway Spruce Forest. *Forest Ecology and Management*. 242, 306-313.

Jurgensen, M. F., Larsen, M. J., and Harvey, A. E. (1980). *Microbial Processes Associated with Nitrogen Cycling in Northern Rocky Forest Soils*. USDA Forest Service, General Technical Report INT-90, pp 175-188.

Jurgensen, M. F., Larsen, M. J., Spano, S. D., Harvey, A. E., and Gale, M. R. (1984). Nitrogen Fixation Associated with Increased Wood Decay in Douglas-fir Residue. *Forest Science*. 30, 1038-1044.

Jurgensen, M. F., Larsen, M. J., Graham, R. T., and Harvey, A. E. (1987). Nitrogen Fixation in Woody Residue of Northern Rocky Mountain Conifer Forests. *Canadian Journal of Forest Research*. 17, 1283-1288.

Jurgensen, M. F., Larsen, M. J., Wolosiewicz, M., and Harvey, A. E. (1989). A Comparison of Dinitrogen Fixation Rates in Wood Litter Decayed by White-Rot and Brown-Rot Fungi. *Plant and Soil*. 115, 117-122.

Jurgensen, M. F., Harvey, A. E., Graham, R. T., Page-Dumroese, D. S., Tonn, J. R., Larsen, M. J., and Jain, T. B. (1997). Impacts of Timber Harvesting on Soil Organic Matter, Nitrogen, Productivity, and Health of Inland Northwest Forests. *Forest Science*. 43, 234-251.

Kaiser, L. (1983). Unbiased Estimation in Line-Intercept Sampling. *Biometrics*. 39, 965-976.

Karjalainen, T. (1996). Model Computations on Sequestration of Carbon in Managed Forests and Wood Products under Changing Climatic Conditions in Finland. *Journal of Environmental Management*. 47, 311-328.

Kauppi, P. E., Mielikäinen, K., Kuusela, K. (1992). Biomass and Carbon Budget of European Forests, 1971 to 1990. *Science*. 256, 70-74.

Kazemi, S. M., Dickinson, D. J., and Murphy, R. L. (2001). Effects of Initial Moisture Content on Wood Decay at Different Levels of Gaseous Oxygen Concentrations. *Journal of Agricultural Science and Technology*. 3, 293-304.

Keddy, P. A., and Drummond, C. G. (1996). Ecological Properties for the Evaluation, Management, and Restoration of Temperate Deciduous Forest Ecosystems. *Ecological Applications*. 6, 748-762.

Keith, H., Barrett, D, and Keenan, R. (2000). *Review of Allometric Relationships for Estimating Woody Biomass for New South Wales, the Australian Capital Territory, Victoria, Tasmania and South Australia.* National Carbon Accounting System, Technical Report 5b. The Australian Greenhouse Office.

Keller, E. A., and Swanson, F. J. (1979). Effects of Large Organic Material on Channel Form and Fluvial Processes. *Earth Surface Processes and Landforms.* 4, 361-380.

Keller, M., Alencar, A., Asner, G. P., Braswell, B., Bustamante, M., Davidson, E., Feldpausch, T., Fernandes, E., Goulden, M., Kabat, P., Kruijt, B., Luizão, F., Miller, S., Markewitz, D., Nober, A. D., Nober, C. A., Filho, N. P., da Rocha, H., Dias, P. S., von Randow, C., and Vourlitis, L. (2004a). Ecological Research in the Large-Scale Biosphere-Atmosphere Experiment in Amazonia: Early Results. *Ecological Applications.* 14, S3-S16.

Keller, M., Palace, M., Asner, G. P., Pereira, R., and Silva, J. N. M. (2004b). Coarse Woody Debris in Undisturbed and Logged Forests in the Eastern Brazilian Amazon. *Global Change Biology.* 10, 784-795.

Knox, B., Ladiges, P., Evans, B. (1995). *Biology.* McGraw-Hill Book Company. Sydney, Australia.

Knutson, D. M. (1973). The Bacteria in Sapwood, Wetwood, and Heartwood of Trembling Aspen (*Populus tremuloides*). *Canadian Journal of Botany.* 51, 489-500.

Krankina, O. N., and Harmon, M. E. (1995). Dynamics of the Dead Wood Carbon Pool in Northwestern Russian Boreal Forests. *Water, Air, and Soil Pollution.* 82, 227-238.

Krankina, O. N., Harmon, M. E., Kukuev, Y. A., Treyfeld, R. F., Kashpor, N. N., Kresnov, V. G., Skudin, V. M., Protasov, N. A., Yatskov, M., Spycher, G., and Povarov, W. D. (2002). Coarse Woody Debris in Forest Regions of Russia. *Canadian Journal of Forest Research.* 32, 768-778.

Kraus, T. E. C., Dahlgren, R. A., and Zasoski, R. J. (2003). Tannins in Nutrient Dynamics of Forest Ecosystems - A Review. *Plant and Soil.* 256, 41-66.

Kravchenko, I. K., and Doroshenko, E. V. (2003). Nitrogen-Fixing Activity in Peat Soils from a Raised Bog. *Microbiology.* 72, 98-102.

Laiho, R., and Prescott, C. E. (1999). The Contribution of Coarse Woody Debris to Carbon, Nitrogen, and Phosphorus Cycles in Three Rocky Mountain Coniferous Forests. *Canadian Journal of Forest Research.* 29, 1592-1603.

Lambert, R. L., Lang, G. E., and Reiners, W. A. (1980). Loss of Mass and Chemical Change in Decaying Boles of a Subalpine Balsam Fir Forest. *Ecology.* 61, 1460-1473.

Lang, G. E., and Forman, R. T. T. (1978). Detrital Dynamics in a Mature Oak Forest: Hutcheson Memorial Forest, New Jersey. *Ecology.* 59, 580-595.

Larsen, M. J., Jurgensen, M. F., and Harvey, A. E. (1978). N_2 Fixation Associated with Wood Decayed by some Common Fungi in Western Montana. *Canadian Journal of Forest Research.* 8, 341-345.

Leach, J. G., Orr, L. W., and Christensen, C. (1934). The Interrelationships of Bark Beetles and Blue-Staining Fungi in Felled Norway Pine Timber. *Journal of Agricultural Research.* 49, 315-341.

Leach, J. G., Orr, L. W., and Christensen, C. (1937). Further Studies on the Interrelationship of Insects and Fungi in the Deterioration of Felled Norway Pine Logs. *Journal of Agricultural Research.* 55, 129-140.

Lee, P. C., Crites, S., Nietfeld, M., van Nguyen, H., and Stelfox, J. B. (1997). Characteristics and Origins of Deadwood Material in Aspen-Dominated Boreal Forests. *Ecological Applications.* 7, 691-701.

Li, C. Y. , Massicote, H. B., and Moore, L. V. H. (1992). Nitrogen-Fixing *Bacillus* sp. Associated with Douglas-Fir Tuberculate Ectomycorrhizae. *Plant and Soil.* 140, 35-40.

Liengen, T. (1999). Conversion Factor Between Acetylene Reduction and Nitrogen Fixation in Free-Living Cyanobacteria from High Arctic Habitats. *Canadian Journal of Microbiology.* 45, 223-229.

Lindenmayer, D. B., Incoll, R. D., Cunningham, R. B., and Donnelly, C. F. (1999). Attributes of Logs of the Floor of Australian Mountain Ash (*Eucalyptus regnans*) Forests of Different Ages. *Forest Ecology and Management.* 123, 195-203.

Lindenmayer, D. B., Cunningham, R. B., and Donnelly, C. F., and Franklin, J. F. (2000). Structural Features of Old-Growth Australian Montane Ash Forests. *Forest Ecology and Management.* 134, 189-204.

Lowman, A. A. (1965). The Lethal Effect of Periodic High Temperatures on Certain Lodgepole Pine Slash Decaying Basidiomycetes. *Canadian Journal of Botany.* 43, 334-338.

Lucas, H. A., and Seber, G. A. F. (1977). Estimating Coverage and Particle Density Using the Line Intercept Method. *Biometrika.* 64, 618-622.

Lugo, A. E., and Brown, S. (1992). Tropical Forests as Sinks of Atmospheric Carbon. *Forest Ecology and Management.* 54, 239-256.

Lutes, D. C. (2002). *Assessment of the Line Transect Method: An Examination of the Spatial Patterns of Down and Standing Dead Wood.* In: *Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western Forests* (Technical Coordinators. W. F. Laudenslayer, Jr., P. J. Shea, B. E. Valentine, C. P. Weatherspoon, and T. E. Lisle, pp 665-675), held November 2-4, 1999. U.S. Department of Agriculture Forest Service, Pacific Southwest Research Station, General Technical Report PSW-GTR-181, August 2002. Reno, Nevada.

Mackensen, J., and Bauhus, J. (1999). *The Decay of Coarse Woody Debris. National Carbon Accounting System, Technical Report 6.* The Australian Greenhouse Office.

Mackensen, J., and Bauhus, J. (2003). Density Loss and Respiration Rates in Coarse Woody Debris of *Pinus radiata, Eucalyptus regnans* and *Eucalyptus maculata. Soil Biology and Biochemistry.* 35, 177-186.

Mackensen, J., Bauhus, J., and Webber, E. (2003). Decomposition Rates of Coarse Woody Debris - A Review with Particular Emphasis on Australian Tree Species. *Australian Journal of Botany*. 51, 27-37.

MacMillan, P. C. (1981). Log Decomposition in Donaldson's Woods, Spring Mill State Park, Indiana. *American Midland Naturalist*. 106, 335-344.

MacMillan, P. C. (1988). Decomposition of Coarse Woody Debris in an Old-Growth Indiana Forest. *Canadian Journal of Forest Research*. 18, 1353-1362.

Madigan, M. T., Martinko, J. M., Parker, J. (1997). *Brock - Biology of Microorganisms, 8th Ed.* Prentice Hall. Upper Saddle River, NJ.

Marshall, P. L., and Davis, G. (2002). *Measuring the Length of Coarse Woody Debris*. Forest Service of British Columbia. Extension Note EN-011.

Marshall, P. L., Davis, G., and LeMay, V. M. (2000). *Using Line Intersect Sampling for Coarse Woody Debris*. Forest Service of British Columbia. Technical Report TR-003.

Maser, C., Cline, S. P., Cromack, K. Jr., Trappe, J. M., and Hansen, E. (1988). *What We Know About Large Trees That Fall to the Forest Floor*. In: *From the Forest to the Sea: A Story of Fallen Trees* (Eds. C. Maser, R. F. Tarrant, J. M. Trappe, and J. F. Franklin, pp 25-45). U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-229. Portland, Oregon.

MathSoft Engineering & Education, Inc. (2001). *Mathcad 2001 for Windows*. MathSoft Engineering & Education, Inc. Cambridge, MA, USA.

Mattson, K. G, Swank, W. T., and Waide, J. B. (1987). Decomposition of Woody Debris in a Regenerating, Clearcut Forest in the Southern Appalachians. *Canadian Journal of Forest Research*. 17, 712-721.

Matzek, V., and Vitousek, P. (2003). Nitrogen Fixation in Bryophytes, Lichens, and Decaying Wood along a Soil-Age Gradient in Hawaiian Montane Rain Forest. *Biotropica*. 35, 12-19.

McCullough, H. A. (1948). Plant Succession on Fallen Logs in a Virgin Spruce-Fir Forest. *Ecology*. 29, 508-513.

McElhinny, C. (2005). *Quantifying Stand Structural Complexity in Woodland and Dry Sclerophyll Forest, South-Eastern Australia*. Ph.D. Thesis, School of Resources, Environment and Society, The Australian National University, Canberra,

McElhinny, C., Gibbons, P., and Brack, C. (2006a). An Objective and Quantitative Methodology for Constructing an Index of Stand Structural Complexity. *Forest Ecology and Management*. 235, 54-71.

McElhinny, C., Gibbons, P., Brack, C., and Bauhus, J. (2006b). Fauna-Habitat Relationships: A Basis for Identifying Key Stand Structural Attributes in Temperate Australian Eucalypt Forests and Woodlands. *Pacific Conservation Biology*. 12, 89-110.

McFee, W. W., and Stone, E. L. (1966). The Persistence of Decaying Wood in the Humus Layers of Northern Forests. *Soil Science Society of America Proceedings.* 30, 513-516.

McIntyre, G. A. (1953). Estimation of Plant Density Using Line Transects. *Journal of Ecology.* 41, 319-330.

McKenny, H. J. A., and Kirkpatrick, J. B. (1999). The Role of Fallen Logs in the Regeneration of Tree Species in Tasmanian Mixed Forest. *Australian Journal of Botany.* 47, 745-753.

McKenny, H. C., Keeton, W. S., and Donovan, T. M. (2006). Effects of Structural Complexity Enhancement on Eastern Red-Backed Salamander (*Plethodon cinereus*) Populations in Northern Hardwood Forests. *Forest Ecology and Management.* 230, 186-196.

McKenzie, N., Ryan, P., Fogarty, P., and Wood, J. (2000). *Sampling, Measurement, and Analytical Protocols for Carbon Estimation in Soil, Litter and Coarse Woody Debris.* National Carbon Accounting System, Technical Report 14. The Australian Greenhouse Office.

McMurry, J. (1996). *Organic Chemistry, 4th Ed.* Brooks/Cole Publishing Company, Pacific Grove, California, USA.

Means, J. E., Cromack, K. Jr., and MacMillan, P. C. (1985). Comparison of Decomposition Models Using Wood Density of Douglas-fir Logs. *Canadian Journal of Forest Research.* 15, 1092-1098.

Means, J. E., MacMillan, P. C., and Cromack, K. Jr. (1992). Biomass and Nutrient Content of Douglas-fir Logs and other Detrital Pools in an Old-Growth Forest, Oregon, U.S.A. *Canadian Journal of Forest Research.* 22, 1536-1546.

Medhurst, J. L., Battaglia, M., Cherry, M. L., Hunt, M. A., White, D. A., and Beadle, C. L. (1999). Allometric Relationships for *Eucalyptus nitens* (Deane and Maiden) Maiden Plantations. *Trees.* 14, 91-101.

Meentemeyer, V. (1978). Macroclimate and Lignin Control of Litter Decomposition Rates. *Ecology.* 59, 465-472.

Meggs, J. M. (1996). *Pilot Study of the Effects of Modern Logging Practices on the Decaying-Log Habitat in Wet Eucalypt Forests in South-East Tasmania.* Report to the Tasmanian RFA Environment and Heritage Technical Committee, Forestry Tasmania, Hobart.

Melillo, J. M., Aber, J. D., and Muratore, J. F. (1982). Nitrogen and Lignin Control of Hardwood Leaf Litter Decomposition Dynamics. *Ecology.* 63, 621-626.

Melin, E. (1930). Biological Decomposition of some Types of Litter from North American Forest. *Ecology.* 11, 72-101.

Meredith, D. S. (1960). Further Observations of Fungi Inhabiting Pine Stumps. *Annals of Botany.* 24, 63-78.

Merrill, W., and Cowling, E. B. (1965). Effect of Variation in Nitrogen Content of Wood on Rate of Decay. *Phytopathology*. 55, 1067-1068.

Merrill, W., and Cowling, E. B. (1966a). Role of Nitrogen in Wood Deterioration: Amount and Distribution of Nitrogen in Fungi. *Phytopathology*. 56, 1083-1090.

Merrill, W., and Cowling, E. B. (1966b). Role of Nitrogen in Wood Deterioration: Amounts and Distribution of Nitrogen in Tree Stems. *Canadian Journal of Botany*. 44, 1555-1580.

Millard, S. P., and Neerchal, N. K. (2001). *Environmental Statistics with S-Plus*. CRC Press, Boca Raton, Florida, USA.

Minderman, G. (1968). Addition, Decomposition and Accumulation of Organic Matter in Forests. *Journal of Ecology*. 56, 355-362.

Mishra, U., and Dhar, D. W. (2004). Biodiversity and Biological Degradation of Soil. *Resonance*. January, 26-33.

Moorhead, D. L., and Reynolds, J. F. (1991). A General Model of Litter Decomposition in the Northern Chihuahuan Desert. *Ecological Modelling*. 56, 197-219.

Moorhead, D. L., and Sinsabaugh, R. L. (2000). Simulated Patterns of Litter Decay Predict Patterns of Extracellular Enzyme Activities. *Applied Soil Ecology*. 14, 71-79.

Moorhead, D. L., Sinsabaugh, R. L., Linkins, A. E., and Reynolds, J. F. (1996). Decomposition Processes: Modelling Approaches and Applications. *The Science of the Total Environment*. 183, 137-149.

Morrison, M. L., and Raphael, M. G. (1993). Modeling the Dynamics of Snags. *Ecological Applications*. 3, 322-330.

Nabuurs, G. J., and Mohren, G. M. J. (1995). Modelling Analysis of Potential Carbon Sequestration in Selected Forest Types. *Canadian Journal of Forest Research*. 25, 1157-1172.

Næsset, E. (1999b). Decomposition Rate Constants of *Picea abies* Logs in Southeastern Norway. *Canadian Journal of Forest Research*. 29, 372-381.

Næsset, E. (1999a). Relationship Between Relative Wood Density of *Picea abies* Logs and Simple Classification Systems of Decayed Coarse Woody Debris. *Scandinavian Journal of Forest Research*. 14, 454-461.

Norby, R. J., and Sigal, L. L. (1989). Nitrogen Fixation in the Lichen *Lobaria pulmonaria* in Elevated Atmospheric Carbon Dioxide. *Oecologia*. 79, 566-568.

Nuntagij, A., de Lassus, C., Sayag, D., and Andre, L. (1989). Aerobic Nitrogen Fixation During the Biodegradation of Lignocellulosic Wastes. *Biological Wastes*. 29, 43-62.

O'Connell, A. M., Grove, T. S. (1987). Seasonal Variation in C_2H_2 Reduction (N_2-Fixation) in the Litter Layer of Eucalypt Forests of South-Western Australia.

Soil Biology and Biochemistry. 19, 135-142.

O'Connell, A. M., Grove, T. S. And Malajczuk, N. (1979). Nitrogen Fixation in the Litter Layer of Eucalypt Forests. *Soil Biology and Biochemistry*. 11, 681-682.

O'Hehir, J. F., and Leech, J. W. (1997). Logging Residue Assessment by Line Intersect Sampling. *Australian Forestry*. 60, 196-201.

Olson, J. S. (1963). Energy Storage and the Balance of Producers and Decomposers in Ecological Systems. *Ecology*. 44, 322-331.

Oreskes, N., Shrader-Frechette, K., and Belitz, K. (1994). Verification, Validation, and Confirmation of Numerical Models in the Earth Sciences. *Science*. 263, 641-646.

Parnas, H. (1975). Model for Decomposition of Organic Material by Microorganisms. *Soil Biology and Biochemistry*. 7, 161-169.

Paulsrud, P. (2001). *The Nostoc Symbiont of Lichens: Diversity, Specificity and Cellular Modifications*. Ph.D. Thesis, Department of Physiological Botany, Uppsala University, Sweden.

Pérez, C. A., Carmona, M. R., Aravena, J. C., and Armesto, J. J. (2004). Successional Changes in Soil Nitrogen Availability, Non-Symbiotic Nitrogen Fixation and Carbon/Nitrogen Ratios in Southern Chilean Forest Ecosystems. *Oecologia*. 140, 617-625.

Pickford, S. G., and Hazard, J. W. (1978). Simulation Studies on Line Intersect Sampling of Forest Residue. *Forest Science*. 24, 469-483.

Plantinga, A. J., and Birdsey, R. A. (1993). Carbon Fluxes Resulting from U.S. Private Timberland Management. *Climatic Change*. 23, 37-53.

Polglase, P. J., and Attiwill, P. M. (1992). Nitrogen and Phosphorus Cycling in Relation to Stand Age of *Eucalyptus regnans* F. Muell. *Plant and Soil*. 142, 157-166.

Preston, C. M., Trofymow, J. A., Niu, J., and Sayer, B. (1997). ^{13}C Nuclear Magnetic Resonance Spectroscopy with Cross-Polarization and Magic-Angle Spinning Investigation of the Proximate-Analysis Fractions Used to Assess Litter Quality in Decomposition Studies. *Canadian Journal of Botany*. 75, 1601-1613.

Preston, C. M., Trofymow, J. A., Niu, J., and Fyfe, C. A. (2002). Harvesting and Climate Effects on Organic Matter Characteristics in British Columbia Coastal Forests. *Journal of Environmental Quality*. 31, 402-413.

Preston, C. M., Bhatti, J. S., Flanagan, L. B., and Norris, C. (2006). Stocks, Chemistry, and Sensitivity to Climate Change of Dead Organic Matter Along the Canadian Boreal Forest Transect Case Study. *Climatic Change*. 74, 223-251.

Pyle, C., and Brown, M. M. (1998). A Rapid System of Decay Classification for Hardwood Logs of the Eastern Deciduous Forest Floor. *Journal of the Torrey Botanical Society*. 125, 237-245.

Pyle, C., and Brown, M. M. (1999). Heterogeneity of Wood Decay Classes within Hardwood Logs. *Forest Ecology and Management.* 114, 253-259.

Renshaw, E. (1995). *Modelling Biological Populations in Space and Time.* Cambridge University Press, Cambridge.

Rice, A. H., Pyle, E. H., Saleska, S. R., Hutyra, L., Palace, M., Keller, M., de Camargo, P. B., Portilho, K., Marques, D. F., and Wofsy, S. C. (2004). Carbon Balance and Vegetation Dynamics in an Old-Growth Amazonian Forest. *Ecological Applications.* 14, S55-S71.

Ringvall, A., and Ståhl, G. (1999a). Field Aspects of Line Intersect Sampling for Assessing Coarse Woody Debris. *Forest Ecology and Management.* 119, 163-170.

Ringvall, A., and Ståhl, G. (1999b). On the Field Performance of Transect Relascope Sampling for Assessing Downed Coarse Woody Debris. *Scandinavian Journal of Forest Research.* 14, 552-557.

Ringvall, A., Ståhl, G., Teichmann, V., Gove, J. H., and Ducey, M. J. (2001). Two-Phase Approaches to Point and Transect Relascope Sampling of Downed Logs. *Canadian Journal of Forest Research.* 31, 971-977.

Robertson, A. I., Bunn, S. E., Boon, P. I., and Walker, K. F. (2000). Sources, Sinks and Transformations of Organic Carbon in Australian Floodplain Rivers. *Marine and Freshwater Research.* 50, 813-829.

Rose, A. K. (2000). Coarse *Woody Debris and Nutrient Dynamics in a Southern Appalachian Spruce-fir Forest.* Masters Thesis. University of Tennessee, Knoxville.

Roskoski, J. P. (1980). Nitrogen Fixation in Hardwood Forests of the Northeastern United States. *Plant and Soil.* 54, 33-44.

Roskoski, J. P. (1981). Comparative C_2H_2 Reduction and $^{15}N_2$ Fixation in Deciduous Wood Litter. *Soil Biology and Biochemistry.* 13, 83-85.

Rowland, a. P., and Roberts, J. D. (1999). Evaluation of Lignin and Lignin-Nitrogen Fractionation Following Alternative Detergent Fiber Pre-treatment Methods. *Communications in Soil Science and Plant Analysis.* 30, 279-292.

Saldarriaga, J. G., West, D. C., Tharp, M. L., and Uhl, C. (1988). Long-Term Chronosequence of Forest Succession in the Upper Rio Negro of Columbia and Venezuela. *Journal of Ecology.* 76, 938-958.

Salisbury, F. B., and Ross, C. W. (1992). *Plant Physiology, 4th Ed.* Wadsworth Publishing Company. Belmont, California.

Sampson, R. N., Apps , M., Brown , S., Cole , C. V. , Downing , J., Heath , L. S. , Ojima , D. S. , Smith , T. M. , Solomon , A. M., and Wisniewski , J. (1993). Workshop Summary Statement: Terrestrial Biospheric Carbon Fluxes Quantification Of Sinks And Sources Of CO_2. *Water, Air, and Soil Pollution.* 70, 3-15.

Savely, H. E. Jr. (1939). Ecological Relations of Certain Animals in Dead Pine and Oak Logs. *Ecological Monographs*. 9, 321-385.

Saxena, D. K., and Harinder. (2004). Uses of Bryophytes. *Resonance*. June, 56-65.

Scheffer, T. C. (1957). Decay Resistance of Western Redcedar. *Journal of Forestry*. 55, 434-442.

Scheffer, T. C., and Cowling, E. B. (1966). Natural Resistance of Wood to Microbial Deterioration. *Annual Revue of Phytopathology*. 4, 147-170.

Schimel, J. P., and Firestone, M. K. (1989). Inorganic N Incorporation by Coniferous Forest Floor Material. *Soil Biology and Biochemistry*. 21, 41-46.

Schink, B., Ward, J. C., and Zeikus, J. B. (1981). Microbiology of Wetwood: Role of Anaerobic Bacterial Populations in Living Trees. *Journal of General Microbiology*. 123, 313-322.

Schowalter, T. D. (1992). Heterogeneity of Decomposition and Nutrient Dynamics of Oak (*Quercus*) Logs During the First 2 Years of Decomposition. *Canadian Journal of Forest Research*. 22, 161-166.

Schowalter, T. D., Zhang, Y. L., and Sabin, T. E. (1998). Decomposition and Nutrient Dynamics of Oak *Quercus* spp. Logs After Five Years of Decomposition. *Ecography*. 21, 3-10.

Seastedt, T. R., and Crossley, D. A. Jr. (1981). Microarthropod Response Following Cable Logging and Clear-Cutting in the Southern Appalachians. *Ecology*. 62, 126-135.

Sedell, J. R., Bisson, P. A., Swanson, F. J., and Gregory, S. V. (1988). *What We Know About Large Trees That Fall Into Streams and Rivers*. In: *From the Forest to the Sea: A Story of Fallen Trees* (Eds. C. Maser, R. F. Tarrant, J. M. Trappe, and J. F. Franklin, pp 47-81). U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-229. Portland, Oregon.

Sedjo, R. A. (1992). Temperate Forest Ecosystems in the Global Carbon Cycle. *Ambio*. 21, 274-277.

Seidler, R. J., Aho, P. E., Raju, P. M., and Evans, H. J. (1972). Nitrogen Fixation by Bacterial Isolates from Decay in Living White Fir Trees (*Abies concolor* (Gord. and Glend.) Lindl.). *Journal of General Microbiology*. 73, 413-416.

Shang, B. Z., He, H. S., Crow, T. R., and Shifley, S. R. (2004). Fuel Load Reductions and Fire Risk in Central Hardwood Forests of the United States: A Spatial Simulation Study. *Ecological Modelling*. 180, 89-102.

Sharp, R. F., and Millbank, J. W. (1973). Nitrogen Fixation in Deteriorating Wood. *Experimentia*. 29, 895-896.

Shifley, S. R., Thompson III, F. R., Dijak, W. D., Larson, M. A., and Millspaugh, J. J. (2006). Simulated Effects of Forest Management Alternatives on Landscape Structure and Habitat Suitability in the Midwestern United States. *Forest Ecology*

and Management. 229, 361-377.

Silvester, W. B., Sollins, P., Verhoeven, T., and Cline, S. P. (1982). Nitrogen Fixation and Acetylene Reduction in Decaying Conifer Boles: Effects of Incubation Time, Aeration, and Moisture Content. *Canadian Journal of Forest Research*. 12, 646-652.

Sinclair, A. R. E., Fryxell, J. M., and Caughley, G. (2006). *Wildlife Ecology, Conservation, and Management*, 2nd Ed. Blackwell Publishing Ltd, Malden, Massachusetts, USA.

Sinsabaugh, R. L., Antibus, R. K., and Linkins, A. E. (1991). An Enzymic Approach to the Analysis of Microbial Activity during Plant Litter Decomposition. *Agriculture, Ecosystems and Environment*. 34, 43-54.

Sinsabaugh, R. L., Antibus, R. K., Linkins, A. E., McClaugherty, C. A., Rayburn, L., Repert, D., and Weiland, T. (1992). Wood Decomposition Over a First-Order Watershed: Mass Loss as a Function of Lignocellulase Activity. *Soil Biology and Biochemistry*. 24, 743-749.

Snedecor, G. W., and Cochran, W. G. (1980). *Statistical Methods, 7th Edition*. The Iowa State University Press. Ames, Iowa, USA.

Snowdon, P., Eamus, D., Gibbons, P., Khanna, P. K., Keith, H., Raison, R. J., and Kirschbaum, M. U. F. (2000). *Biomass Sampling Strategies*. National Carbon Accounting System, Technical Report 17. The Australian Greenhouse Office.

Söderström, L. (1988). Sequence of Bryophytes and Lichens in Relation to Substrate Variables of Decaying Coniferous Wood in Northern Sweden. *Nordic Journal of Botany*. 8, 89-97.

Sokal, R. R., and Rohlf, F. J. (1995). *Biometry: The Principles and Practice of Statistics in Biological Research, 3rd Edition*. W. H. Freeman and Company, New York.

Sollins, P. (1982). Input and Decay of Coarse Woody Debris in Coniferous Stands in Western Oregon and Washington. *Canadian Journal of Forest Research*. 12, 18-28.

Sollins, P., Cline, S. P., Verhoeven, T., Sachs, D., and Spycher, G. (1987). Patterns of Log Decay in Old-Growth Douglas-fir Forests. *Canadian Journal of Forest Research*. 17, 1585-1595.

Spain, A. V. (1984). Litterfall and the Standing Crop of Litter in Three Tropical Australian Rainforests. *Journal of Ecology*. 72, 947-961.

Spano, S. D., Jurgensen, M. F., Larsen, M. J., and Harvey, A. E. (1982). Nitrogen-Fixing Bacteria in Douglas-fir Residue Decayed by *Fomitopsis pinicola*. *Plant and Soil*. 68, 117-123.

Specht, R. L. (1970). *Vegetation*. In: *The Australian Environment, 4th Ed* (Ed. G. W. Leeper, pp 44-67). Melbourne University Press, Melbourne, Australia.

Sperry, J. S., Hacke, U. G., and Pittermann, J. (2006). Size and Function in Conifer Tracheids and Angiosperm Vessels. *American Journal of Botany*. 93, 1490-1500.

Spetich, M. A., Shifley, S. R., and Parker, G. R. (1999). Regional Distribution and Dynamics of Coarse Woody Debris in Midwestern Old-Growth Forests. *Forest Science*. 45, 302-313.

Spies, T. A., and Cline, S. P. (1988). *Coarse Woody Debris in Forests and Plantations of Coastal Oregon*. In: *From the Forest to the Sea: A Story of Fallen Trees* (Eds. C. Maser, R. F. Tarrant, J. M. Trappe, and J. F. Franklin, pp 5-24). U.S. Department of Agriculture Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-229. Portland, Oregon.

Spies, T. A., Franklin, J. F., and Thomas, T. B. (1988). Coarse Woody Debris in Douglas-fir Forests of Western Oregon and Washington. *Ecology*. 69, 1689-1702.

Ståhl, G. (1998). Transect Relascope Sampling - A Method for the Quantification of Coarse Woody Debris. *Forest Science*. 44, 58-63.

Ståhl, G., Ringvall, A., Gove, J. H., and Ducey, M. J. (2002). Correction for Slope in Point and Transect Relascope Sampling on Downed Coarse Woody Debris. *Forest Science*. 48, 85-92.

Stevenson, S. K., Jull, M. J., and Rogers, B. R. (2006). Abundance and Attributes of Wildlife Trees and Coarse Woody Debris at Three Silvicultural Systems Study Areas in the Interior Cedar-Hemlock Zone, British Columbia. *Forest Ecology and Management*. 233, 176-191.

Stewart, G. H., and Burrows, L. E. (1994). Coarse Woody Debris in Old-Growth Temperate Beech (*Nothofagus*) Forests of New Zealand. *Canadian Journal of Forest Research*. 24, 1989-1996.

Stewart, H. T. L., and Flinn, D. W. (1985). Nutrient Losses from Broadcast Burning Of *Eucalyptus* Debris in North-east Victoria. *Australian Forest Research*. 15, 321-332.

Stokland, J. N., and Sippola, A-L. (2004). *Monitoring Protocol for Wood-Inhabiting Fungi in the Alberta Biodiversity Monitoring Program*. Report for the Alberta Biodiversity Monitoring Program. Version 2.9, 20/12/2004.

Struyf, A., Hubert, M., and Rousseeuw, P. J. (1997). Integrating Robust Clustering Techniques in S-PLUS. *Computational Statistics & Data Analysis*. 26, 17-37.

Sturtevant, B. R., Bissonette, J. A., Long, J. N., and Roberts, D. W. (1997). Coarse Woody Debris as a Function of Age, Stand Structure, and Disturbance in Boreal Newfoundland. *Ecological Applications*. 7, 702-712.

Swift, M. J. (1977). The Ecology of Wood Decomposition. *Science Progress*. 64, 175-199.

Swift, M. J., Healey, I. N., Hibberd, J. K, Sykes, J. M., Bampoe, V., and Nesbitt, M. E. (1976). The Decomposition of Branch-Wood in the Canopy and Floor of a Mixed Deciduous Woodland. *Oecologia*. 26, 139-149.

Swift, M. J., Boddy, L., and Healey, I. N. (1984). Wood Decomposition in an Abandoned Beech and Oak Coppiced Woodland in South-east England, II. The Standing Crop of Wood on the Forest Floor with Particular Reference to its Invasion

by *Tipula flavolineata* and other Animals. *Holarctic Ecology*. 7, 218-228.

Tabak, H. H., and Cooke, W. B. (1968). The Effects of Gaseous Environments on the Growth and Metabolism of Fungi. *Botanical Review*. 34, 126-252.

Tainter, F. H., and McMinn, J. W. (1999). *Early Deterioration of Coarse Woody Debris'*. General Technical Report - Southern Research Station, USDA Forest Service. No. SRS-30, pp 232-237.

Tajchman, S., Benyon, R., Bren, L., Kochenderfer, J., and Pan, C. (1996). On Spatial Variability of Above-Ground Forest Biomass. *Biomass and Bioenergy*. 11, 383-386.

Temnuhin, V. B. (1996). Preliminary Quantitative Estimation of Wood Decomposition by Fungi in a Russian Temperate Pine Forest. *Forest Ecology and Management*. 81, 249-257.

Tietje, W. D., Waddell, K. L., Vreeland, J. K., and Bolsinger, C. L. (2002). Coarse Woody Debris in Oak Woodlands of California *Western Journal of Applied Forestry*. 17, 139-146.

Tinker, D. B., and Knight, D. H. (2001). Temporal and Spatial Dynamics of Coarse Woody Debris in Harvested and Unharvested Lodgepole Pine Forests. *Ecological Modelling*. 141, 125-149.

Torres, J. A. (1994). Wood Decomposition of *Cyrilla racemiflora* in a Tropical Montane Forest. *Biotropica*. 26, 124-140.

Triska, F. J., and Cromack, K. Jr. (1980). *The Role of Woody Debris in Forests and Streams*. In: *Forests, Fresh Perspectives from Ecosystem Analysis* (Ed. R. H. Waring, pp 171-190). Proceedings of the 40th Biology Colloquium (1979). Corvallis, Oregon, Oregon State University Press.

Tsavkelova, E. A., Lobakova, E. S., Kolomeitseva, G. L., Cherdyntseva, T. A., and Netrusov, A. I. (2003a). Associative Cyanobacteria Isolated from the Roots of Epiphytic Orchids. *Microbiology*. 72, 92-97.

Tsavkelova, E. A., Lobakova, E. S., Kolomeitseva, G. L., Cherdyntseva, T. A., and Netrusov, A. I. (2003b). Localization of Associative Cyanobacteria on the Roots of Epiphytic Orchids. *Microbiology*. 72, 86-91.

Turnbull, C. R. A., and Madden, J. L. (1986). Litter Accession, Accumulation and Decomposition in Cool Temperate Forests of Southern Tasmania. *Australian Forest Research*. 16, 145-153.

Turner, J. (1986). Organic Matter Accumulation in a Series of *Eucalyptus grandis* Plantations. *Forest Ecology and Management*. 17, 231-242.

Uhl, C., and Kauffman, J. B. (1990). Deforestation, Fire Susceptibility, and Potential Tree Response to Fire in the Eastern Amazon. *Ecology*. 71, 437-449.

Underwood, A. J. (1997). *Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance*. Cambridge University Press.

Urcelay, C., and Robledo, G. (2004). Community Structure of Polypores (Basidiomycetes) In Andean Alder Wood in Argentina: Functional Groups among Wood-Decay Fungi? *Austral Ecology*. 29, 471-476.

USDA Forest Service. (2001). *Down Woody Debris and Fuels*. In: *Field Inventory and Analysis Field Methods for Phase 3 Measurements, 2001, Section 14*. USDA Forest Service. http://fia.fs.fed.us/manuals/p3sec14_2001.doc

Van Lear, D. H. (1996). *Dynamics of Coarse Woody Debris in Southern Forest Ecosystems*. In: *Biodiversity and Coarse Woody Debris in Southern Forests*. Proceedings of the Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity (Eds. J. W. McMinn and D. A. Crossley Jr., pp 10-17).

van Wagner, C. E. (1968). The Line Intersect Method in Forest Fuel Sampling. *Forest Science*. 14, 20-26.

van Wagner, C. E. (1982). *Practical Aspects of the Line Intersect Method*. Information Report PI-X-12. Petawawa National Forestry Institute. Canadian Forestry Service, Chalk River, Ontario, Canada.

van Wagner, C. E., and Wilson, A. L. (1976). Diameter Measurement in the Line Intersect Method. *Forest Science*. 22, 230-232.

Venables, W. N., and Ripley, B. D. (2000). *Modern Applied Statistics with S-Plus. 3rd Ed* (corrected second printing). Springer-Verlag, New York.

Vitousek, P. M., and Howarth, R. W. (1991). Nitrogen Limitation on Land and in the Sea: How Can it Occur? *Biogeochemistry*. 13, 87-115.

Vitousek, P. M., and Matson, P. A. (1984). Mechanisms of Nitrogen Retention in Forest Ecosystems: A Field Experiment. *Science*. 225, 51-52.

Waddell, K. L. (2002). Sampling Coarse Woody Debris for Multiple Attributes in Extensive Resource Inventories. *Ecological Indicators*. 1, 139-153.

Wang, C., Bond-Lamberty, B., and Gower, S. T. (2002). Environmental Controls on Carbon Dioxide Flux from Black Spruce Coarse Woody Debris. *Oecologia*. 132, 374-381.

Warren, W. G., and Olsen, P. F. (1964). A Line Intersect Technique for Assessing Logging Waste. *Forest Science*. 10, 267-276.

Watson, G. S. (1971). Estimating Functionals of Particle Size Distributions. *Biometrika*. 58, 483-490.

Wells, J. M., and Boddy, L. (1990). Wood Decay, and Phosphorus and Fungal Biomass Allocation, in Mycelial Cord Systems. *New Phytologist*. 116, 285-295.

Wells, J. M., Hughes, C., and Boddy, L. (1990). The Fate of Soil-Derived Phosphorus in Mycelial Cord Systems of *Phanerochaete velutina* and *Phallus impudicus*. *New Phytologist*. 114, 595-606.

Wermelinger, B., Duelli, P., and Obrist, M. K. (2003). *Windthrow Stimulates Arthropod Biodiversity in Forests*. In: *Dead Wood: A Key to Biodiversity* (Ed. F.

Mason, G. Nardi, and M. Tisato., pp 79-82). Proceedings of the International Symposium 29th 31st May 2003. Mantova, Italy.

Whiles, M. R., and Grubaugh, J. W. (1996). *Importance of Coarse Woody Debris to Southern Forest Herpetofauna.* In: *Biodiversity and Coarse Woody Debris in Southern Forests.* Proceedings of the Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity (Eds. J. W. McMinn and D. A. Crossley Jr., pp 94-100).

Whitford, W. G., Meentemeyer, V., Seastedt, T. R., Cromack, K. Jr., Crossley, D. A. Jr., Santos, P., Todd, R. L., and Waide, J. B. (1981). Exceptions to the AET Model: Deserts and Clear-Cut Forest. *Ecology.* 62, 275-277.

Widmer, F., Shaffer, B. T., Porteous, L. A., and Seidler, R. J. (1999). Analysis of nifH Gene Pool Complexity in Soil and Litter at a Douglas Fir Forest Site in the Oregon Cascade Mountain Range. *Applied and Environmental Microbiology.* 65, 374-380.

Wieder, R. K., and Lang, G. E. (1982). A Critique of the Analytical Methods Used in Determining Decomposition Data Obtained from Litter Bags. *Ecology.* 63, 1636-1642.

Wikström, P., and Eriksson, L. O. (2000). Solving the Stand Management Problem Under Biodiversity-Related Considerations. *Forest Ecology and Management.* 126, 361-376.

Wilkes, J. (1982). Pattern and Process of Heartrot in *Eucalyptus microcorys. Australian Forestry.* 45, 51-56.

Witkamp, M., and Van der Drift, J. (1961). Breakdown of Forest Litter in Relation to Environmental Factors. *Plant and Soil.* 15, 295-311.

Witty, J. L. (1979). *Overestimate of N_2-Fixation in the Rhizosphere by the Acetylene Reduction Method.* In: *The Soil-Root Interface* (Eds. J. L. Harley and R. S. Russell., pp 137-144). Academic Press, London.

Woldendorp, G. (2000). *Estimating Carbon in Mature Eucalypt Forests.* Honours Thesis, Department of Geography. School of Resource Management and Environmental Science, The Australian National University.

Woldendorp, G., and Keenan, R. J. (2005). Coarse Woody Debris in Australian Forest Ecosystems: A Review. *Austral Ecology.* 30, 834-843.

Woldendorp, G., Spencer, R. D., Keenan, R. J., and Barry, S. (2002b). *An Analysis of Sampling Methods for Coarse Woody Debris in Australian Forest Ecosystems.* Bureau of Rural Sciences, Australia. A Report for the National Greenhouse Strategy, Module 6.6 (Criteria and Indicators of Sustainable Forest Management), November 2002.

Woldendorp, G., Keenan, R., and Ryan, M. (2002a). *Coarse Woody Debris in Australian Forest Ecosystems.* A Report for the National Greenhouse Strategy, Module 6.6 (Criteria and Indicators of Sustainable Forest Management), April 2002. Bureau of Rural Sciences, Department of Agriculture Fisheries & Forestry, Australia.

Woldendorp, G., Keenan, R. J., Barry, S., and Spencer, R. D. (2004). Analysis of Sampling Methods for Coarse Woody Debris. *Forest Ecology and Management.* 198, 133-148.

Woodall, C. W., and Nagel, L. M. (2006). Coarse Woody Type: A New Method for Analyzing Coarse Woody Debris and Forest Change. *Forest Ecology and Management.* 227, 115-121.

Woods, P. V., and Raison, R. J. (1982). An Appraisal of Techniques for the Study of Litter Decomposition in Eucalypt Forests. *Australian Journal of Ecology.* 7, 215-225.

Wyatt, J. T., and Silver, J. K. G. (1969). Nitrogen Fixation by *Gloeocapsa. Science.* 165, 908-909.

Yee, M., Yuan, Z.-Q., and Mohammed, C. (2001). Not Just Waste Wood: Decaying Logs as Key Habitats in Tasmania's Wet Sclerophyll *Eucalyptus obliqua* Production Forests: the Ecology of Large and Small Logs Compared. *Tasforests.* 13 (1), 119-128.

Yee, M., Grove, S. J., Richardson, A. M. M., and Mohammed, C. L. (2006). *Brown Rot in Inner Heartwood: Why Large Logs Support Characteristic Saproxylic Beetle Assemblages of Conservation Concern.* In: *Insect Biodiversity and Dead Wood: Proceedings of a Symposium for the 22nd International Congress of Entomology* (Eds. S. J. Grove and J. L. Hanula. pp 42-56). Gen. Tech. Rep. SRS-93. Asheville, NC, U.S. Department of Agriculture, Forest Service, Southern Research Station.

Yoneda, T. (1975). Studies on the Rate of Decay of Wood Litter on the Forest Floor. I. Some Physical Properties of Decaying Wood. *Japanese Journal of Ecology.* 25, 40-46.

Youngblood, A., Metlen, K. L., and Coe, K. (2006). Changes in Stand Structure and Composition after Restoration Treatments in Low Elevation Dry Forests of Northern Oregon. *Forest Ecology and Management.* 234, 143-463.

Zackrisson, O., DeLuca, T. H., Nilsson, M-C., Sellstedt, A., and Berglund, L. M. (2004). Nitrogen Fixation Increases with Successional Age in Boreal Forests. *Ecology.* 85, 3327-3334.

Zar, J. H. (1996). *Biostatistical Analysis, 3rd Edition.* Prentice-Hall International, Inc.

APPENDIX A

PARAMETRIC CORRECTION FOR ASPECT

Aspect has traditionally not been a significant factor in determining decay rates of CWD. However, this may be the result of the nominal nature of traditional measurements of aspect, especially with non-parametric tests being less powerful than parametric tests (Sokal and Rohlf 1995, Zar 1996). To adequately test for the interaction of aspect with decay rates of CWD, a method of aspect enumeration was developed (see Figure A-1); which I refer to as 'parametric-aspect'. The method enumerates aspect with respect to the equator; with the direction facing the equator with the lowest value, and the direction facing away from the equator with the highest value. The pattern of the relative values (lowest value facing equator) was chosen so that they compliment the effect of latitude. This is based on the idea that lower aspect values (facing the equator) provide similar conditions to lower latitude values (nearer the equator). The underlying assumption here is that lower aspect values and lower latitudes provide warmer conditions than environments with higher aspect values and higher latitudes. This complimentary design of the parametric-aspect with latitude, allows for the analysis of aspect-latitude interactions, especially synergistic interactions.

As aspect is expected to increase in ecological-importance as latitude increases, a measure of the importance of the aspect could be calculated by multiplying the parametric-aspect with the latitude. Since parametric-aspect is unit-less (not measured in degrees, unlike aspect which is traditionally given in degrees), and latitude is measured in degrees, it is proposed that the aspect-importance be given in units of "aspect-latitude degrees". Not only does this 'aspect-importance' incorporate the importance of latitude, but also incorporates the importance of aspect, as high-values (nearer a value of '9'; facing away from the equator) will show the affect of light-availability and heat-availability increasing in importance as they are more likely to become limiting with high parametric-aspect values.

However, it must be mentioned that there is the possibility of errors in this calculation of aspect-importance, as a site in the tropics with parametric-aspect value of '9' may have a higher calculated aspect-importance value than a site outside the tropics (extra tropical) with a parametric-aspect value of '5'. For example, a tropical site at

latitude 15° with parametric-aspect of 9 will have an aspect-importance of 135 aspect-latitude degrees, while a sub-tropical site at latitude 25° with a parametric-aspect value of 5 will have an aspect-importance value of 125 aspect-latitude degrees. It is unclear whether the aspect-latitude interaction at the tropical site really would be more ecologically important than the interaction at the sub-tropical site. However, it is unlikely that any error in using this calculation of aspect-importance would amount to any significant errors, as the aspect-importance is a relative-measure, which would not induce problems in the majority of usage.

Calculation of the parametric-aspect requires a different formula for each hemisphere (see Figure A-1); see Equation A-1 for the southern hemisphere calculation, and Equation A-2 for the northern hemisphere calculation. The formulae provided are for calculations with measurements in degrees (not northings and eastings), as this is the unit of measurement used in field readings obtained from a compass. (Often GPS-units do not work in the understorey of dense forest environments, and a compass must be used, with direction provided only in degrees.)

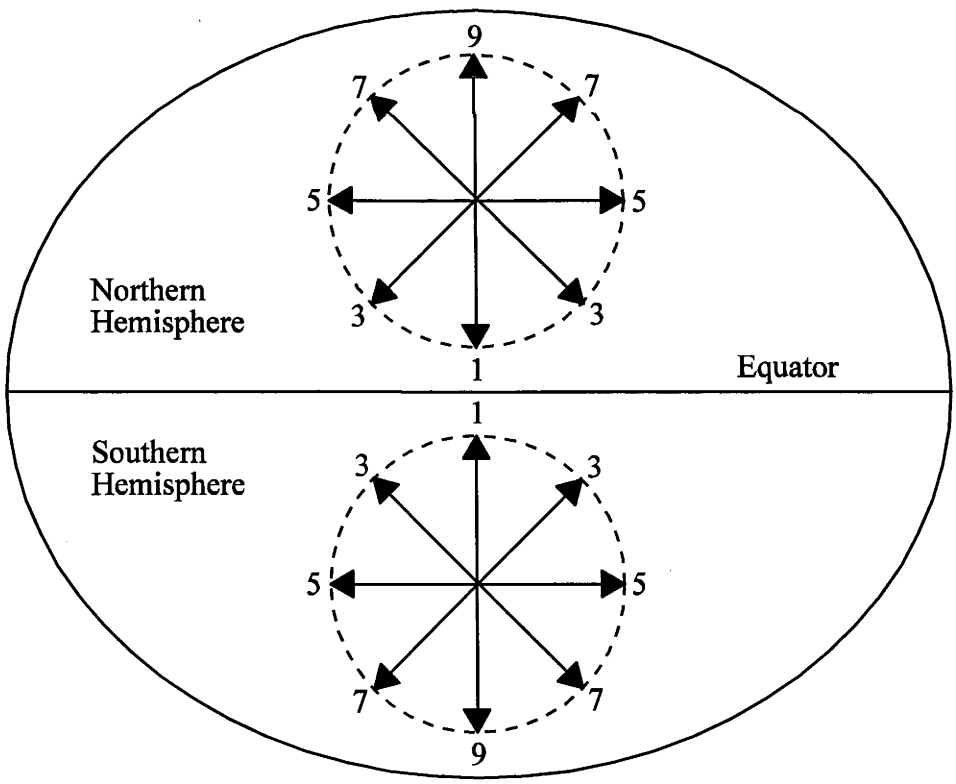


Figure A-1. Diagrammatic representation of the philosophy behind the 'parametric-aspect' determination. (See Equation A-1 and Equation A-2 for formulae to calculate the parametric-aspect for each hemisphere.)

SOUTHERN HEMISPHERE PARAMETRIC-ASPECT CALCULATION

$$A_{dec} = 9 - \frac{\left|A_{\deg_S} - 180\right|}{22.5}$$

Equation A-1

Where: A_{dec} = parametric-aspect,

$A_{\deg_S}$ = direction (in degrees) for Southern Hemisphere readings,

| | = absolute value.

NORTHERN HEMISPHERE PARAMETRIC -ASPECT CALCULATION

$$A_{dec} = 1 + \frac{\left|A_{\deg_N} - 180\right|}{22.5}$$

Equation A-2

Where: A_{dec} = parametric-aspect,

$A_{\deg_N}$ = direction (in degrees) for Northern Hemisphere readings,

| | = absolute value.

APPENDIX B

CORRECTION FOR SLOPE

The following is the mathematical formulae and proof for the conversion of traversed-distance to an equivalent horizontal-distance, as discussed in the Methods chapter (Chapter 3); section 3.4.1.4 *Correction for Slope*.

The following calculation for the transect equivalent horizontal distance is for a transect running in a single direction only. If the transect consists of two or more segments in different directions, then the EHD of each segment will have to be calculated separately. (For a multiple direction (multiple segment) line-transect, T, the transect length as used below, becomes the transect segment-length.)

The value of b in Figure B-1 is the minor axis of the ellipse, and is in the direction of the aspect. The value for b can be calculated as shown in Figure B-2. The major axis, a, has no decrease in magnitude due to the affect of slope, as it is perpendicular to the aspect, and as such a = T.

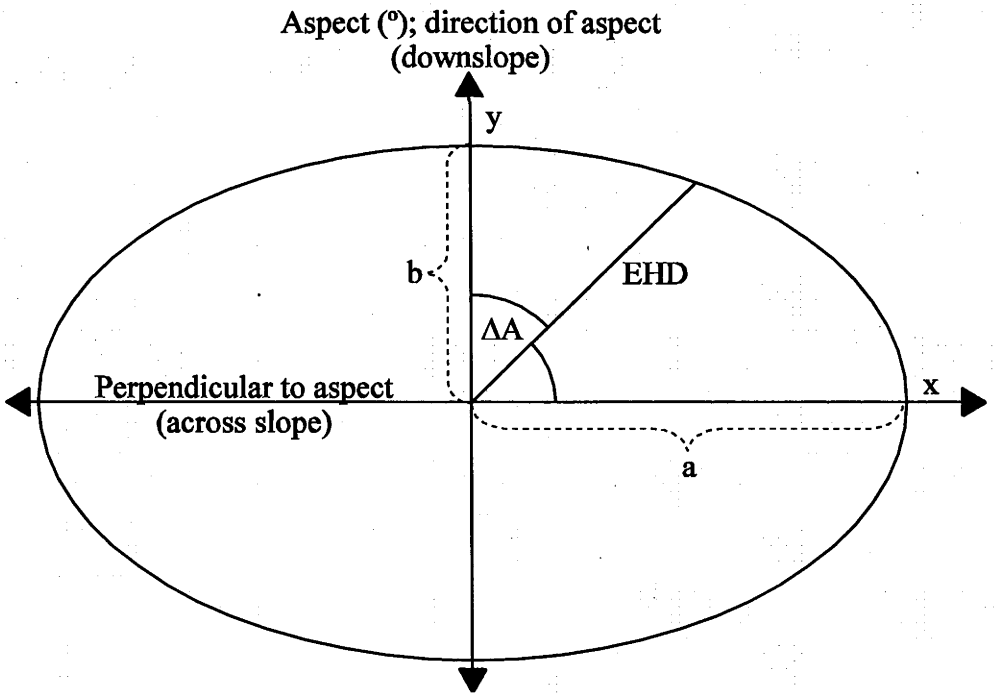


Figure B-1. The ellipse created by the affect slope has on the length of the line-transect. EHD is the equivalent horizontal distance of the line-transect, *a* is the value of the major axis, *b* is the value of the minor axis, ΔA is the angular deviation of the line-transect from aspect direction. (Note that θ = 90°-ΔA.)

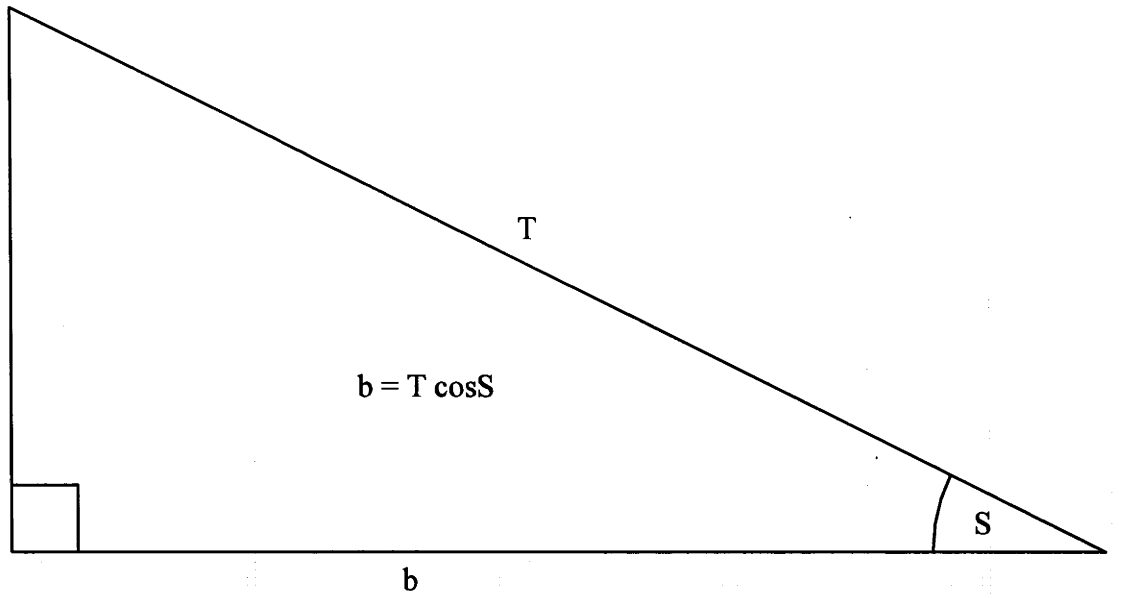


Figure B-2. The calculation of the minor axis of the ellipse formed by the affect of slope on the line-transect.

Substituting r (the 'radius') for EHD, we get the variables as shown in Figure B-3. All values can be represented in the first quadrant of the ellipse (see Figure B-3).

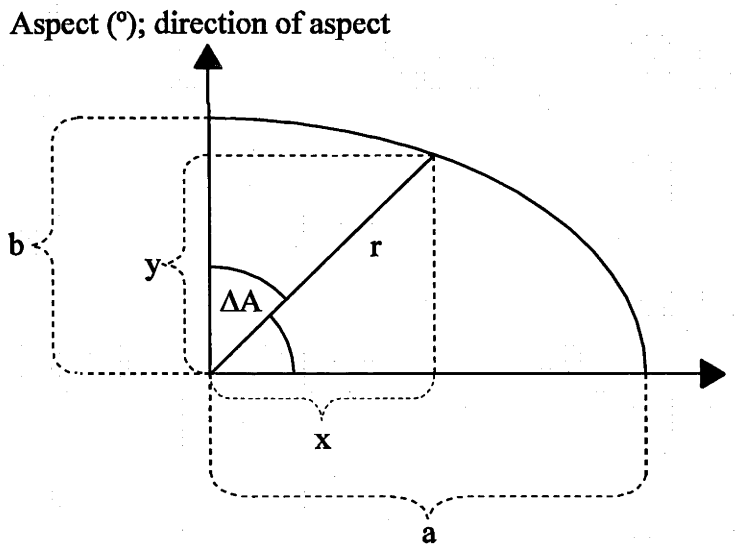


Figure B-3. First quadrant representation of the effect slope has on line-transect length. ΔA is the angular deviation of the line-transect from aspect direction (note that θ = 90°-ΔA), *a* is the value of the major axis, *b* is the value of the minor axis, and r is the 'radius', and is equivalent to the equivalent horizontal distance (EHD).

The formula for the ellipse of Figure B-1 is:

$$\frac{x^2}{a^2}+\frac{y^2}{b^2}=1 \qquad \textbf{Equation B-1}$$

Where: x = the rectangular co-ordinate value of the line-transect length in the direction perpendicular to aspect (m), and is equal to r.cos θ,

y = the rectangular co-ordinate value of the line-transect length in the direction of aspect (m), and is equal to r.sin θ,

a = the length of the major axis (m), and is equal to T,

b = the length of the minor axis (m), and is equal to T cosS (see Figure B-2),

By substitution, we get the series:

$$\frac{b^2x^2}{a^2b^2}+\frac{a^2y^2}{a^2b^2}=1 \qquad \textbf{Equation B-2}$$

$$\frac{b^2x^2+a^2y^2}{a^2b^2}=1 \qquad \textbf{Equation B-3}$$

Substituting for x^2 and y^2 we get:

$$\frac{b^2(r.\cos\vartheta)^2+a^2(r.\sin\vartheta)^2}{a^2b^2}=1 \qquad \textbf{Equation B-4}$$

$$\frac{b^2r^2\cos^2\vartheta+a^2r^2\sin^2\vartheta}{a^2b^2}=1 \qquad \textbf{Equation B-5}$$

$$\frac{r^2\left(b^2\cos^2\vartheta+a^2\sin^2\vartheta\right)}{a^2b^2}=1 \qquad \textbf{Equation B-6}$$

$$r^2=\frac{a^2b^2}{b^2\cos^2\vartheta+a^2\sin^2\vartheta} \qquad \textbf{Equation B-7}$$

$$r=\sqrt{\frac{a^2b^2}{b^2\cos^2\vartheta+a^2\sin^2\vartheta}} \qquad \textbf{Equation B-8}$$

Substituting EHD for r, T for a, T cosS for b, and 90°-ΔA for θ, we get the following series.

$$EHD=\sqrt{\frac{T^2(T.\cos S)^2}{(T.\cos S)^2\cos^2(90°-\Delta A)+T^2\sin^2(90°-\Delta A)}} \qquad \textbf{Equation B-9}$$

$$EHD=\sqrt{\frac{T^2T^2.\cos^2S}{T^2.\cos^2S.\cos^2(90°-\Delta A)+T^2\sin^2(90°-\Delta A)}} \qquad \textbf{Equation B-10}$$

$$EHD=\sqrt{\frac{T^2T^2.\cos^2S}{T^2\left[\cos^2S.\cos^2(90°-\Delta A)+\sin^2(90°-\Delta A)\right]}} \qquad \textbf{Equation B-11}$$

$$EHD = \sqrt{\frac{T^2.\cos^2 S}{\cos^2 S.\cos^2(90° - \Delta A) + \sin^2(90° - \Delta A)}}$$ **Equation B-12**

Where: T = the length (m) of the transect (or transect segment),

S = the slope (°) in the direction of aspect,

ΔA = the deviation of the transect direction from that of the aspect (°).

For the purposes of calculator or computer use, the following interpretation of the above formula may be easier to use:

$$EHD = \sqrt{\frac{T^2.(\cos S)^2}{(\cos S)^2.[\cos(90° - \Delta A)]^2 + [\sin(90° - \Delta A)]^2}}$$ **Equation B-13**

APPENDIX C

DECAY CLASS DETERMINATION

Table C-1. Parameter classification values used in coding CWD for cluster analysis.

DECAY CLASS CLASSIFICATION (4-digit)		Score
LOG DENSITY	Solid	1000
	Porous (deforms when hit)	2000
	Crumbles (breaks when hit)	3000
SHAPE	Intact	100
	Flattening out	200
	Rubble on ground	300
BARK	Intact	10
	Some loss	20
	Total loss	30
CRACKS	Nil	1
	Surface	2
	Deep	3
	Splitting	4

An attempt was made to define decay classes specific to for the forests studied. The need for this arose when a predetermined decay class system failed to describe the CWD encountered adequately during the first sampling period in the wet eucalypt forest site of southern NSW. A method of describing external characteristics was developed from the observed external characteristics noted during the NSW sampling. The method devised is as shown in Table C-1. The system is used by summing the individual scores from the four parameters (characteristics), resulting in a four-digit code. This method was, of course, only available for the subsequent sampling periods in southern Tasmania (also wet eucalypt forest), central Queensland (dry eucalypt woodland), and northern Queensland (tropical rainforest). The example analysis presented here is the analysis for the wet eucalypt forests of southern Tasmania, as the analyses for the Queensland sampling was performed in the same manner. The statistical package S-PLUS was used for the cluster analyses, with the non-hierarchical *pam* (partitioning around medoids) algorithm used (Struyf *et al.* 1997; S-PLUS 6.1 documentation).

From the graphical outputs, it was decided that the three-, four-, and five-group systems should be investigated. The output of the analysis, including all 128 samples, showed a three-, four-, or five-class system can be used for the decay class classification (**Table C-2**). As most of the samples were in coupes which were exposed to a slash burn after logging (n = 91), it was decided to repeat the analysis with these samples. The resulting output (**Table C-3**) shows that either a three- or four-class system can be used to classify the burnt-post-logging samples, but the five-class system became

unstable. Each of the sample groups with the coding 1131, 1132, and 1133, were split between classes two and three. Therefore, it was decided that the choice of decay class system had to be either the three- or four-class system. As the four-class system offers higher resolution between CWD groupings, it was decided that this is the best system to use. The graphical output of the four-class system can be seen in Figure C-1. It must be noted, however, that the samples not exposed to a slash burn have been exposed to forest fires, although the burning intensity is unknown.

The clustering analyses did not include samples from the most decayed CWD group, as none existed in the sampling area; sampling was done in areas of known logging dates. As this class must be included in any system of decay classification, it was decided that this most-decayed class should be appended to the four-class system accepted, creating a five-class system. The 'decision tree' constructed from the distinguishing features of the analyses is shown in Table C-4.

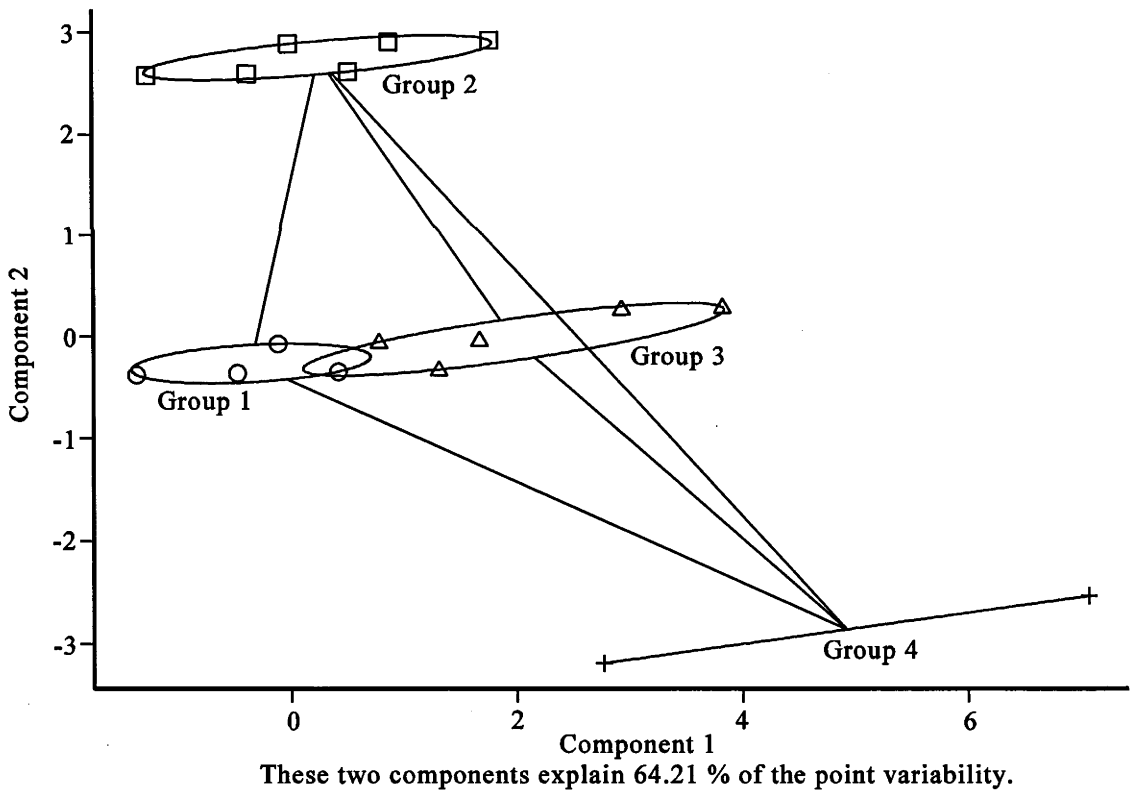


Figure C-1. Visual output of the four-class system adopted for CWD of the wet eucalypt forests of southern Tasmania. The graphical output is for all samples. The groups are the decay classes (Groups 1-4 respectively represent decay classes 1-4).

Table C-2. Groupings of southern Tasmanian wet eucalypt forest samples into three, four, and five decay classes based upon external characteristics (n = 128). The analyses are of CWD sampled in coupes that includes both slash-burn and non slash-burn treatments.

Code:	1121	1122	1123	1131	1132	1133	1134	1232	2121	2122	2123	2131	2132	2133	3133	3134	3234
n:	1	7	1	18	58	13	1	1	1	2	2	3	5	10	2	2	1
Groups:																	
3	1			2				3	1			2					3
4	1			2			3	4	1			2	3				4
5	1			2	3		4	5	1			2	4				5

Table C-3. Groupings of southern Tasmanian wet eucalypt forest samples into three, four, and five decay classes based on external characteristics (n = 91). The analyses are of CWD that were exposed to a slash burn after clearfelling. (Groupings with asterisks show sample-coding that overlapped groups.)

Code:	1121	1122	1131		1132		1133		1232	2121	2131	2132	2133
n:	1	2	7	8	14	39	6	1	1	1	3	4	4
Groups:													
3	1		2						3	1	2		
4	1		2						3	1	4		
5	1		2*	3*	2*	3*	2*	3*	4	1	5		

Table C-4. The 'decision tree' used to classify the CWD of wet eucalypt forests into a five-class decay stage system. The system was based on *E. obliqua* forest in southern Tasmania.

PARAMETER	QUESTION	DECISION
Shape	Is the log rubble on the ground?	Yes = decay class 5, else continue to next question.
	Is the log flattening out?	Yes = decay class 4, else continue to next question.
Bark	Is there any bark remaining?	Yes = decay class 1, else continue to next question.
Cracks	Is the log splitting apart?	Yes = decay class 3, else continue to next question.
	Are there any sort of cracks present?	No = decay class 2, else continue to next question.
Log Density	Is the log solid or soft?	Solid = decay class 2. Soft = decay class 3.

APPENDIX D

DOUBLE-EXPONENTIAL MODEL OF DECAY

The double-exponential model of decay (DEM) has the form

$$\frac{Q_t}{Q_0} = w.e^{-k_1.t} + (1-w)e^{-k_2.t}$$

Equation D-1

Where: $\frac{Q_t}{Q_0}$ = Relative proportion remaining at time *t*,

w = Relative proportion of labile-component,

k_1 = Decay-constant of labile-component,

1-w = Relative proportion of recalcitrant-component,

k_2 = Decay-constant of recalcitrant-component.

The single-exponential model of decay (SEM) has the form

$$\frac{Q_t}{Q_0} = e^{-k.t}$$

Equation D-2

Where: $\frac{Q_t}{Q_0}$ = Relative proportion remaining at time *t*,

k = Decay-constant.

The SEM is a general model that describes decay with a single exponential term. There is no w-parameter, as the SEM describes the whole component, resulting in a w-value of 1; therefore, the w-parameter is omitted from the SEM.

A problem with the DEM is in the interpretation of the output, with respect as to what the two exponential-terms are actually describing; for a discussion of problems with the DEM see section 2.2.5.8 *Discussion — Comparison of Models*. The SEM has been used to describe the decay of the species studied in this project (see section 4.2 *Decay Rates*), and the DEM-values are only presented here for completeness. The analysis of this project's data with the DEM is in no way to be interpreted as condoning the use of the DEM; it is provided purely for the use of readers whom may want these values for comparison with other work.

The values chosen for the initialisation of the DEM *w*-parameter for the eucalypts of southern Tasmania and NSW South Coast were taken from the model of Medhurst *et al.* (1999), which was for *Eucalyptus nitens* (Deane & Maiden) Maiden. Although *E. nitens* was not studied in this project, this paper was the only paper found with dual-parameters, for a eucalypt species, that would provide input into the DEM. A problem with the model of Medhurst *et al.* (1999) is that it is inaccurate for diameters greater than 50cm (see Figure D-1). The diameter-values chosen for the range-of-diameters of Figure D-1 is realistic, as *E. nitens* can attain a height of 80-90m (Brooker and Kleinig 1999, Costermans 2000). Since the minimum-diameter for this project was 10cm (definition of CWD), and the maximum diameter of reasonable accuracy of Medhurst *et al.* (1999) is 50cm, this was chosen as the range for the adoption of the initialisation-value for the w-parameter (using sapwood proportion) for the eucalypt species, with the median value (30cm) used to initialise the *w*-parameter (see Table D-1). The *w*-parameter for the rainforest species of Queensland was arbitrarily chosen as 0.5. The initialisation values for the k_1 and k_2 parameters for the DEM were chosen to envelop the *k*-value determined from the SEM analyses (see section 4.2 *Decay Rates*); with k_1 (representing the labile-component) having a greater value (in magnitude) than the SEM *k*-value, and k_2 (representing the recalcitrant-component) having a smaller value (see Table E-1 for an expanded description).

The DEM-curves (Figure D-3) for the eucalypts in the wet eucalypt forests show little difference from the SEM-curves. This lack of difference is undoubtedly due to the very slow decay of the eucalypts. The faster-decomposing tropical rainforest species show a marked difference between the curves of the DEM and SEM. However, the DEM showed overall slower decay than the SEM, and this appears to contradict the accepted decay-dynamics of these very humid rainforests in the wet tropics. At least in this instance, it appears that the SEM is describing the decay-dynamics of the fast-decaying tropical rainforest species better than the DEM. (The difference in k_1 and k_2 for the rainforest species appears to be too large to make sense biologically; it would appear that either the SEM or a multi-exponential model with more than two exponential-terms should be used for the rainforest data.)

Slow-decaying species, such as the eucalypts, do not benefit from using the double-exponential model, as the fitted model will not be appreciably different from the single-exponential model. The k_1 and k_2 parameters of the DEM (for the eucalypts) are

so similar in value (to each other and the SEM *k*-value), that the fitted DEM-curve almost completely overlaps the fitted SEM-curve.

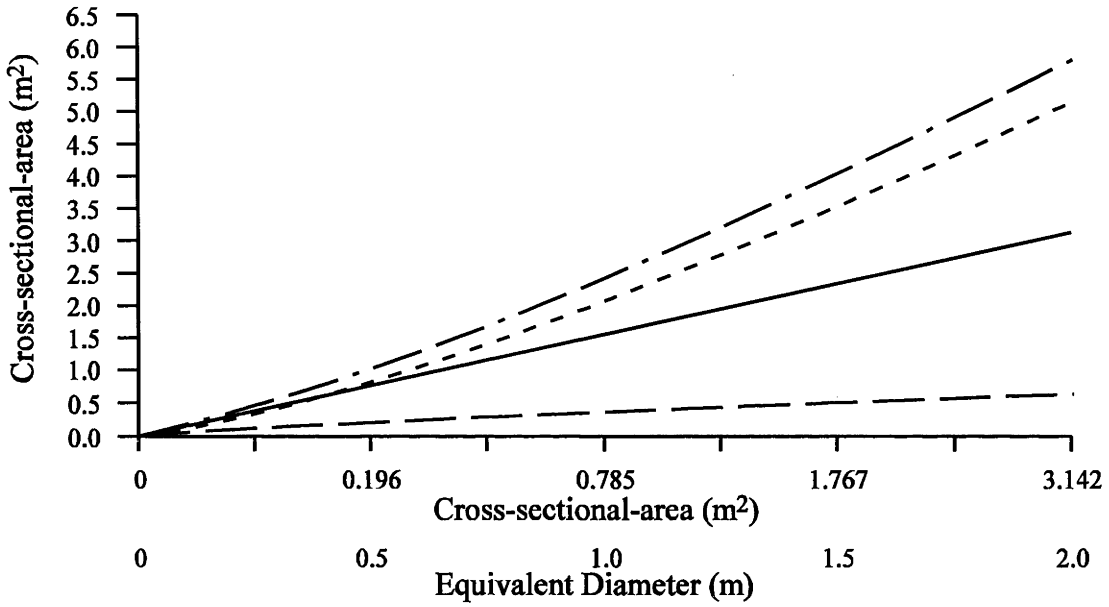


Figure D-1. Graph of the model of Medhurst *et al.* (1999) showing acceptable accuracy up to 50cm diameter; and increasing inaccuracy for diameters greater than 50cm. The diameter-range shown is reasonable for *E. nitens* (see text for justification of the diameter-range). The dashed-curve (— —) is the sapwood, the dotted-curve (- - -) is the heartwood, and the dot-dash curve (— - — - —) is the sapwood+heartwood. The solid-line (———) is the cross-sectional-area; this has a 1:1 relationship with the horizontal axis, and is the path the model-generated sapwood+heartwood curve should take.

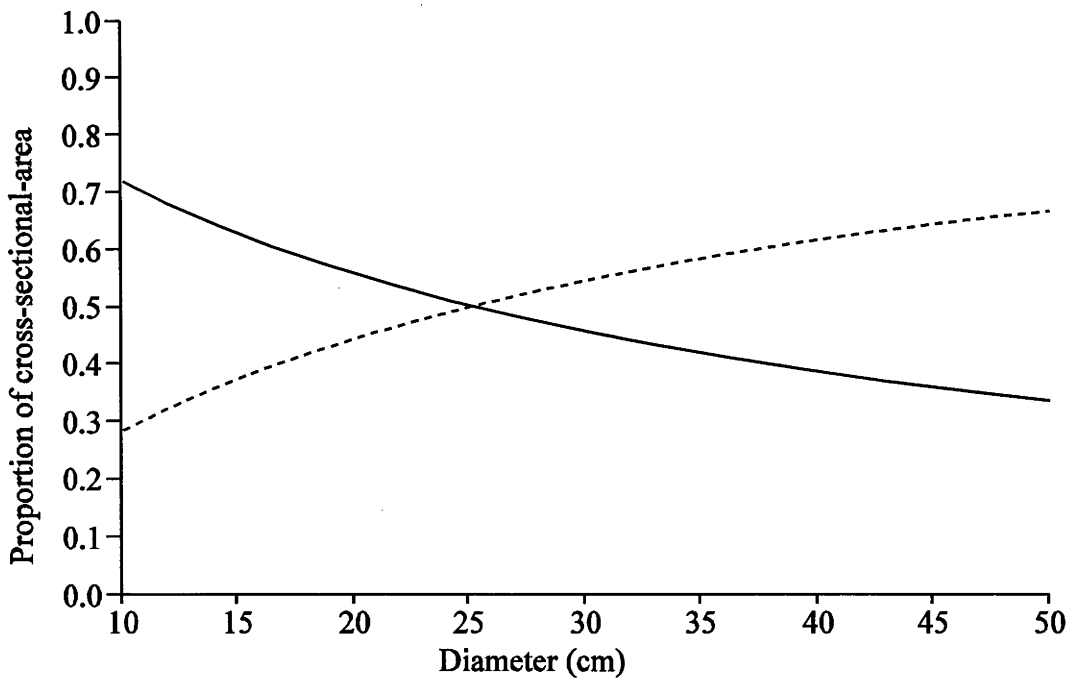


Figure D-2. The relative proportions of sapwood and heartwood; derived from the model of Medhurst *et al.* (1999) for *E. nitens*.

Table D-1. The parameter-initialisation and analyses returned-values for the DEM analyses.

SEM *k*-values as determined by the analyses of Section 4.2:

	Southern Tasmania	NSW South Coast	Far North Queensland
k	0.007228	0.005538	0.1121

DEM initialisation-values as determined by the SEM *k*-values:

	Southern Tasmania	NSW South Coast	Far North Queensland
w	0.457	0.457	0.5
k_1	0.1	0.1	0.2
k_2	0.01	0.01	0.01

Initialisation *w*-values for the Tasmanian and NSW eucalypts were based on the model of Medhurst *et al.* (1999); their model is for sapwood vs. heartwood, and the representative-diameter chosen is 30cm. The *w* initialisation-value for the Queensland rainforest species was arbitrarily set as 0.5.

Initialisation decay-constant values (k_1 and k_2) were chosen by the following method:

Southern Tasmania
- $k_1 < k_{SEM} < k_2 \rightarrow$ **0.1 < 0.007228 < 0.01**

NSW South Coast
- $k_1 < k_{SEM} < k_2 \rightarrow$ **0.1 < 0.005538 < 0.01**

Far North Queensland
- $k_1 < k_{SEM} < k_2 \rightarrow$ **0.2 < 0.1121 < 0.01**

DEM returned-values as determined by the DEM analyses:

	Southern Tasmania	NSW South Coast	Far North Queensland
w	0.569332	0.494993	0.238839
k_1	-0.007391	-0.007350	-28.893437
k_2	-0.006592	-0.003846	-0.065409

For fast-decaying species, such as the tropical rainforest species of FNQ, the DEM may be useful, as it does show a marked difference between the fitted DEM and SEM curves. Of course, the FNQ DEM-values, due to a large number of species being in the dataset, may not be showing dual-parameter decay dynamics, it may be showing individual *k*-values between two very different groups of plants; where the difference may exist at the Family or Order level, or may even be environmentally determined. That is, it may be showing one group of slower-decomposing species that possess high levels of powerful-toxins, and another group of faster-decomposing species with lower concentrations, or lesser-strength, toxins. It may even be showing the difference between densities, where one group with less-dense wood may have its toxins leached

rapidly, and the other group has its toxins leached at a much slower rate. The same argument for the toxins would apply to nutrients, but with more-concentrated nutrients or slower leaching of nutrients leading to faster rates of decay. It is this lack of knowledge, of the parameters being expressed by the DEM, which makes it unwieldy to interpret; for a discussion of problems with the DEM see section 2.2.5.8 *Discussion — Comparison of Models*.

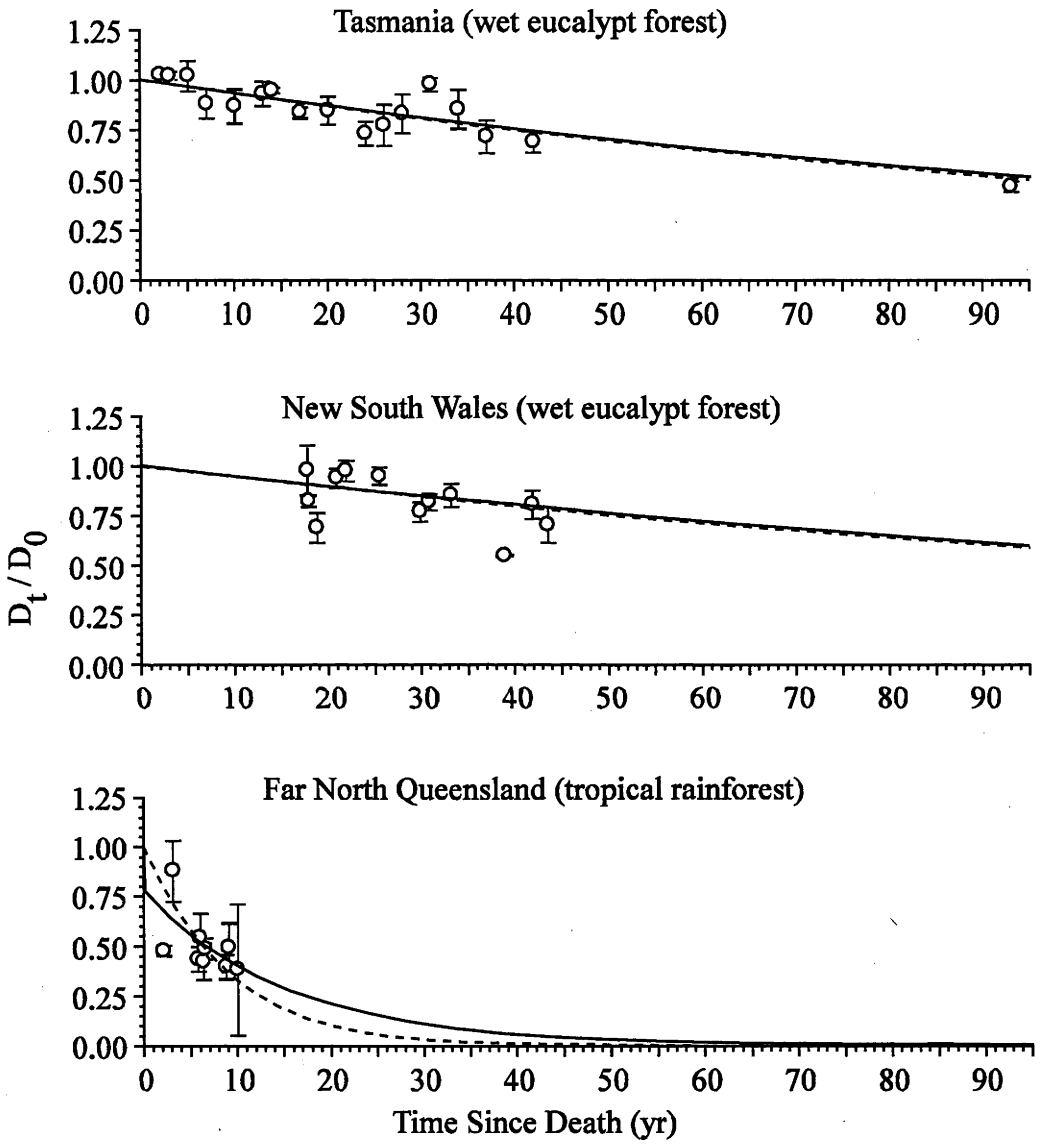


Figure D-3. Double-exponential model (DEM; ——) vs. single-exponential model (SEM; - - -). Note that the DEM and SEM curves are almost identical for the slow-decaying eucalypts in the wet eucalypt forests. Also note the curve for the DEM of Far North Queensland does start at the proportion of 1.00; it appears to start at 0.76 because the proportion of the fast-decaying labile-component (*k1* = -28.893437) has a proportion of almost 0.24 (*w* = 0.238839); see Table E-1 for method used.